Conflict monitoring and motor control during pre-potent response suppression in aging: A behavioral, kinematic, and electrophysiological investigation

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ABSTRACT

Conflict monitoring and motor control during pre-potent response suppression in aging: A behavioral, kinematic, and electrophysiological investigation

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The current thesis investigated the cognitive mechanisms that contribute to age-related declines in pre-potent response suppression, and the interaction between those mechanisms and motor control processes that support response production. To achieve this goal, participants were visually cued to perform repeated pairs of key presses that established a pre-potent response. This was contrasted with responses that conflicted with the pre-potent pair. Cognitive and motor processes were delineated through kinematic analyses that decomposed reaction time into movement planning and execution phases. The goal of Study 1 was to explore whether there are age differences in conflict adaptation effects during pre-potent response suppression. In this study, conflicts were presented once, twice, or three times in each sequence. Older adults performed the first conflicting response in a series as well as young adults, but at a cost to pre-potent response performance. Younger adults improved performance with increased conflict frequency, whereas older adults did not. Older adults spent less time planning, but more time executing their conflicting responses compared to younger adults. This study revealed that conflict adaptation effects are diminished in the elderly, and that flexible adjustments in motor control by younger adults contribute to age-related differences in pre-potent response suppression. In Study 2, the neurophysiological correlates of conflict monitoring, and their relation to adjustments in motor control were investigated with

concurrent acquisition of motion capture and event-related potential (ERP) data. Context effects were also explored through manipulation of the proportion of conflicting responses across conditions. The movement patterns, and ERP data revealed larger conflict-related interference effects for both groups when the proportion of conflicting responses was low. This context effect was exaggerated in the elderly. Moreover, only younger adults showed a robust conflict-related N2 component over fronto-central electrode sites. The magnitude of this N2 was related to shorter execution time in the younger, but not older participants, indicating that conflict detection facilitated within-trial adjustments in movement control. These findings are discussed in terms of current models of cognitive control and aging. These data contribute to current knowledge about the mechanisms by which conflict monitoring and cognitive control processes influence motor performance.

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CONTRIBUTIONS OF AUTHORS

This dissertation consists of two studies:

Study 1:

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Study 2:

Trewartha, K. M., Penhune, V. B., & Li, K. Z. H. (in preparation). Age differences in pre-potent response suppression investigated using concurrent motion capture and event-related potential recordings.

Relative Contributions

I developed the goals and experimental designs of the current experiments under the guidance of Dr. Karen Li, and Dr. Virginia Penhune. For Study 1, I worked closely with computer programmer Alejandro Endo to create the stimulus presentation program and data analysis tools. All participants were recruited and tested by me, with assistance from undergraduate student Gohar Tajik. For study 2, I created the stimulus presentation program, and modified previous data analysis tools. The response trigger system for synchronizing the motion capture and electrophysiological data was built and designed by engineer David Munro, with my instruction. The participants were recruited and tested by research assistant Michael Spilka, with my guidance. I was responsible for data entry, processing, statistical analyses and interpretation for both studies, with guidance from Drs. Li, Penhune, and Dr. Natalie Phillips. And finally, I wrote both manuscripts with feedback from Drs. Li and Penhune.

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LIST OF ABBREVIATIONS

ACC=	Anterior Cingulate Cortex
ANOVA=	Analysis of Variance
CCA=	Conflict-Control-Adapt
dlPFC	Dorsolateral Prefrontal Cortex
DMC=	Dual-Mechanisms of Control
EEG=	Electroencephalography/Electroencephalogram
EOG=	Electrooculogram
ERN=	Error-Related Negativity
ERP=	Event-Related Potential
fMRI=	Functional Magnetic Resonance Imaging
IRI=	Inter-Stimulus Interval
LRP=	Lateralized Readiness Potential
M1=	Primary Motor Cortex
PFC=	Prefrontal Cortex
Pre-SMA=	Pre-Supplementary Motor Area
RT=	Reaction Time
SMA=	Supplementary Motor Area
TMS=	Transcranial Magnetic Stimulation

Chapter 1: General Introduction

One of the most important characteristics of human behaviour is that we are able to flexibly adapt to the variety of contexts in which our thoughts and actions are performed. The act of driving a motor vehicle offers an excellent everyday example to demonstrate this point. Imagine yourself driving along a busy street. Despite the multitude of distractions both inside and outside of the car, you proceed through an almost automatic series of actions to obey the rules of the road. When a child suddenly runs out into the street, you have only a split second to reprogram the set of actions you were performing in order to avoid hitting the child. In order for us to be able to respond to an anomaly such as this, the cognitive system must be equipped to detect the problem and recruit resources to rapidly adjust our actions. This ability to flexibly adapt our actions likely changes in later adulthood. It is well known that healthy aging is associated with declines in both cognitive and motor processes that are integral to the performance of complex tasks such as driving. In fact, older adults are aware that their cognitive and physical status affects their ability to drive (see Anstey, Wood, Lord, & Walker, 2005). What is less obvious from introspection is the extent to which cognitive and motor control processes interact to support the performance of such tasks. Research has revealed a great deal about the nature of within-domain changes in cognitive and motor control processes that occur in later adulthood. However, we are only beginning to understand the complex way in which those processes interact to produce observed behaviours in complex cognitive/motor tasks. This dissertation explores age differences in the interaction between cognitive mechanisms for detecting conflict in the information-processing stream, and the motor processes involved in modifying our actions.

To achieve this goal, we developed a paradigm that requires participants to make habitual as well as unexpected/conflicting motor responses. In a previous experiment (Trewartha, Endo, Li, & Penhune, 2009) we recorded movement trajectories using 3-D motion capture in order to explore movement patterns of younger and older adults on the habitual and conflicting responses. This study is summarized in more detail later on. Briefly, we found that age-related declines in the performance of conflicting responses were related to older adults' reduced ability to use conflicting information to trigger adjustments in movement execution speed compared to younger adults. That is, younger but not older adults were able to exert cognitive control over motor performance following the presentation of a conflicting stimulus. The nature of this age-related change in the interaction between cognitive and motor processes is explored further in the two current experiments. The first experiment was designed to explore whether older adults could benefit from increased frequency of exposure to conflict. That is, would older adults be able to use conflicting information in order to adapt their responses in a way similar to younger adults if they simply encountered those conflicts more often? For the second experiment we used concurrent recording of movement trajectories, and electroencephalography (EEG) in order to explore the neurophysiological correlates of the cognitive mechanisms involved in detecting response conflict, and to directly explore their relation to movement patterns of younger and older adults. This combination provides important insight into the neural mechanisms associated with the detection of response conflict, and flexible modulation of actions. The following is a review of the background literature pertinent to age-related changes in cognitive and motor processes

that are thought to be involved in managing response conflict, and to the specific methodologies employed in the current experiments.

1.1 Cognitive aging

For the better part of 40 years, psychologists in the cognitive aging field have amassed an extensive literature on the cognitive changes that characterize the normal, healthy aging process (Craik & Salthouse, 2008; Park & Schwarz, 2000). Aside from documenting those age-related declines in performance on a variety of tasks, this literature attempts to explain those changes. Many of those explanations have relied on the argument that we operate with a limited pool of cognitive/attentional resources to perform cognitive tasks (Kahneman, 1973), and that the quantity of those resources declines with age (Hasher & Zacks, 1979; Park, 2000). Such cognitive resource views have led to a variety of common cause hypotheses to explain the observed declines on a variety of cognitive tasks. In particular, common cause theories attribute age-related cognitive decline to general cognitive slowing (e.g., Salthouse, 1996), working memory declines (e.g., Craik & Byrd, 1982), cognitive inhibition deficits (e.g., Hasher & Zacks, 1988; Hasher, Zacks & May, 1999), sensory decline (e.g., Schneider & Pichora-Fuller, 2000), and frontal lobe mediated executive functioning deficits (e.g., West, 1996).

Given that executive, or cognitive control functions are thought to be integral to the ability to adapt flexibly to varying task situations, the frontal lobe hypothesis of cognitive aging is of particular interest for this dissertation. This theory proposes that the declines that we observe on a variety of tasks are largely attributable to age-related dysfunction of areas in the frontal lobes, especially the prefrontal cortex (PFC). This theory is largely based on observations that older adults tend to perform poorly on tasks

that patients with prefrontal cortical damage also perform poorly. Such tasks are often called frontal lobe tasks and include the Stroop, Wisconsin Card sort, Tower of London, and Simon tasks. Largely, these tasks and others like them rely on cognitive control processes that are thought to be involved in the planning, coordinating, sequencing and monitoring of other cognitive operations (Salthouse, Berish, & Atkinson, 2003).

1.2 Cognitive control and pre-potent response suppression

Cognitive control as a psychological construct is often studied in the laboratory using pre-potent response suppression tasks. Such tasks are so called because they involve some pre-potent tendency to respond in a given way depending on stimulus features. For example, in the classic color-word Stroop paradigm (Stroop 1935), participants are required to name the colour of ink in which color words are printed. This task leads to very rapid responses when the color of ink is congruent with the color word (e.g., 'RED' printed in red ink). However, performance suffers in terms of slowed reaction time (RT) and reduced accuracy when the ink color and color word are incongruent (e.g., 'RED' printed in blue ink). It is generally agreed that interference effects, in the form of performance differences between congruent and incongruent versions of the task, are related to the need for cognitive control. That is, one must use cognitive control processes to overcome the pre-potent tendency to want to read the word in order to correctly indicate the color of ink in which it is printed. Other pre-potent response suppression tasks that have been used frequently to study cognitive control include the Eriksen Flanker task (Eriksen & Eriksen, 1974), Simon task (Simon & Rudell, 1967), Stop-signal paradigm (Logan & Cowan, 1984), and Go/No-go task (Donders, 1868/1969). One of the common elements to all of the pre-potent response

suppression tasks described above is the existence of conflict between a pre-potent tendency to respond in a certain way (e.g., reading, in the Stroop task) and the actual response requirement (e.g., naming the ink color). In healthy younger adults, this conflict leads to interference effects in the form of longer RTs and increased error rates for incongruent trials compared to congruent trials. It is commonly argued that these interference effects are related to the concurrent activation of more than one competing response representation (see e.g., Carter & van Veen, 2007). Thus, when asked to perform a conflict trial, participants must recruit cognitive control to suppress the pre-potent response tendency. This recruitment, and exertion of cognitive control is time consuming, and hence, leads to slower performance.

1.3 Conflict monitoring theory

Although researchers have argued that cognitive control is necessary for pre-potent response suppression it is important to provide a general theory that explains how cognitive control is recruited to support that response suppression. Functional magnetic resonance imaging (fMRI) studies have associated areas in the prefrontal cortex (PFC) with the implementation of cognitive control (e.g., Miller & Cohen, 2001; Smith & Jonides, 1999). Other fMRI studies have revealed that the anterior cingulate cortex (ACC) of the medial frontal lobes is also activated during pre-potent response suppression tasks, particularly during conflict trials. The conflict monitoring theory (Botvinick, Braver, Barch, Carter & Cohen, 2001) unites these findings by proposing that the ACC first monitors for the occurrence of various types of conflict, and then sends a trigger to PFC structures (e.g., dorsolateral prefrontal cortex, dlPFC) to allow for cognitive control implementation. The functional significance of such a conflict

monitoring mechanism is that it allows for flexible adjustments in cognitive control aimed at reducing the influence of subsequently encountered conflict on behaviour.

It is generally argued that conflict can occur when a participant makes a correct or incorrect response during the interference tasks mentioned above. During correct trials the conflict occurs in the form of either the incongruency between stimulus dimensions, or concurrent activation of competing response representations. During error trials, the conflict is thought to be between a representation of the actual response (an error) and the intended, or required response. Alternatively, error trials may lead to a conflict between the error and a rapid correction of that error (see e.g., Carter & van Veen, 2007). For the purpose of this dissertation I will refer to conflict on correct trials as stimulus-related conflict, and conflict on error trials as response-related conflict.

1.4 Neuroimaging support for conflict monitoring theory

Further motivation for the development of the conflict monitoring theory came from observations of electrophysiological correlates of conflict processing. Such electrophysiological correlates of cognitive processes are commonly measured using continuous EEG recordings during the performance of a given task. The continuous stream of EEG data is then segmented according to specific stimulus and/or response events in order to explore characteristic waveforms that are associated with particular cognitive processes. These event-related potentials (ERP) are thus associated with particular cognitive processes depending on the experimental conditions that elicited them. Early observations from two independent electrophysiological laboratories revealed that when participants made performance errors a negative deflection in the ERP signal occurs over fronto-central electrode sites, peaking between 50-100 ms after the

error (Gehring, Coles, Meyer, & Donchin, 1990; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991). This ERP component has been referred to both as the error-related negativity (ERN) and error negativity (Ne) in the literature. For the current purposes I will use the ERN nomenclature. Since those early studies, the ERN has been observed following errors in a variety of types of tasks. For example, the ERN has been observed when individuals make errors during pre-potent responses tasks including the Stroop (e.g., Swick & Turken, 2002), Simon (e.g., Leuthold & Sommer, 1999), Stop-signal (e.g., Kok, Ramautar, de Ruiter, Band, & Ridderinkhof, 2004), and Go/No-go tasks (e.g., Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003). Additionally, many tasks that do not require pre-potent response suppression have demonstrated an ERN on error trials, including sensorimotor adaptation (e.g., Anguera, Seidler, & Gehring, 2009), time estimation (e.g., Miltner, Braun, & Coles, 1997), recognition memory (Curran, DeBuse, & Leynes, 2007), speech production errors (e.g., Möller, Jansma, Rodríguez-Fornells, & Münte, 2007; Trewartha & Phillips, 2011) and others. This seeming ubiquity of experimental contexts in which an ERN has been observed lends credence to the notion of a general error processing system in the brain.

Although ERP studies provide high temporal resolution for studying the time-course of individual cognitive processes, they reveal little about the specific brain areas that generate the electrical activity. Although we do know the scalp location over which the ERP was recorded, this does not clearly pinpoint the location, or orientation of the dipoles that gave rise to that recorded voltage. One method, called dipole source modeling, uses EEG data in order to calculate possible sources of the electrical activity in the brain. Such source modeling techniques have been used to specify the neural

generator of the ERN, and have consistently pointed to the ACC as a likely candidate (e.g., Dehaene, Posner, & Tucker, 1994; Nieuwenhuis, et al., 2003; van Boxtel, van der Molen, & Jennings, 2005; van Veen & Carter, 2002; Yeung, Botvinick, & Cohen, 2004). Corroborative support that the ACC is the source of the ERN, and error detection processes in general, comes from a number of fMRI studies, exploring the brain areas active following errors, compared to correct responses (e.g., Braver, Barch, Gray, Molfese, & Snyder, 2001; Carter, et al., 1998; Garavan, Ross, Kaufman, & Stein, 2003; Mathalon, Whitfield, & Ford, 2003; Ullsperger & von Cramon, 2001). In fact, combined ERP and fMRI studies have shown a correlation between the ERN and ACC activity (e.g., Mathalon, et al., 2003). There is now a large literature corroborating these findings, and it is generally accepted that the ACC plays an important role in monitoring response conflict (see Botvinick, Braver, Yeung, Ullsperger, Carter, & Cohen, 2004 for a review; c.f., Holroyd & Coles, 2002).

Further evidence supporting the conflict monitoring theory of ACC function comes from tasks that involve stimulus-related conflict rather than errors. ERP studies have revealed a number of other conflict-related ERP components that occur prior to the overt response, and are commonly observed on correct trials. These ERP components are thought to reflect the monitoring/detection of conflict between stimulus dimensions, or concurrently activated response representations. One such conflict-related ERP component, the N450, is most commonly observed as a negative waveform peaking approximately 300-500 ms after the presentation of an incongruent stimulus in the Stroop task (e.g., West & Alain, 2000; West, 2003). Like the ERN, the N450 is usually observed over fronto-central sites. This component likely represents the conflict associated with the

competition between the pre-potent response representation (e.g., word reading), and the required response (e.g., color naming) on incongruent trials (West, 2003). Stimulus-related conflict processing has also been associated with other ERP components such as the conflict-related N2 (see Folstein & van Petten, 2008 for review). The N2 is also a negative deflection in the EEG signal over fronto-central sites, peaking approximately 200-350 ms after stimulus presentation. The N2 has been observed in the Go/No-go task (e.g., Falkenstein, Hoormann, & Hohnsbein, 1999), the Flanker task (e.g., Yeung, et al., 2004) and the stop-signal paradigm (e.g., van Boxtel, van der Molen, Jennings & Brunia, 2001). This component is thought to reflect the conflict associated with the need to suppress a planned/anticipated response (see Folstein & van Petten, 2008). Thus, the N2 is likely related to the detection of information about conflict that is important for response preparation processes.

In the search for a neural locus for these stimulus-related conflict monitoring components (i.e., the N2 and N450), source modeling techniques again revealed the ACC as a potential generator (e.g., Nieuwenhuis, et al., 2003; Szücs, Soltész, & White, 2009; van Veen & Carter, 2002; West, 2003). Also, as in the case of the ERN, fMRI studies have consistently revealed activation of the ACC during pre-potent response suppression tasks during conflict trials (for reviews see e.g., Barch, et al., 2001; Botvinick, 2007; Botvinick et al., 2001; Botvinick, et al., 2004). Combined with the ERN literature, these stimulus-related conflict studies further demonstrate the general role of the ACC in monitoring for instances of conflict.

1.5 Aging and pre-potent response suppression

In the cognitive aging literature, there are a large number of studies that have reported age-related cognitive control deficits. Older adults commonly exhibit disproportionately slowed RT, and sometimes increasing error rates compared to younger adults on conflict trials in the Stroop task (e.g., Pilar, Guerrini, Phillips, & Perfect, 2008), the flanker task (e.g., Zeef & Kok, 1993), the Simon task (e.g., van der Lubbe & Verleger, 2002), stop-signal paradigm (e.g., Rush, Barch, & Braver, 2006), and the Go/No-Go task (e.g., Nielson, Garavan, Langenecker, Stein, & Rao, 2001). Together these findings, and others like them, lend support for the idea that the ability to suppress a pre-potent response declines in later adulthood. This is often taken as evidence in support of the idea that aging is associated with specific deficits in cognitive control (e.g., Braver & Barch, 2002). However, as argued above, those tasks require both cognitive control and conflict monitoring processes. Thus, determining the locus of this age-related decline in cognitive control requires further knowledge about age differences in the mechanisms that drive cognitive control adjustments and allow for successful pre-potent response suppression.

1.6 Aging and brain areas associated with cognitive control and conflict monitoring

As mentioned earlier, the frontal lobe dysfunction hypothesis of cognitive aging demonstrated similarities in the performance of cognitive control tasks between neurological patients with frontal lobe damage and older adults (e.g., West, 1996). Researchers have also recently drawn the link between the conflict monitoring abilities of patients with ACC lesions to that of older adults. An important assumption of the conflict monitoring theory is that special populations with neurological pathologies affecting ACC function should experience conflict monitoring deficits. Consistent with this

assumption, there is evidence that conflict monitoring is impaired in patients with schizophrenia and attention deficit hyperactivity disorder (see Carter & van Veen, 2007). Similarly, evidence is growing that older adults (a non-clinical, specialized population) exhibit conflict monitoring dysfunction. In particular, cross-sectional electrophysiological comparisons of younger and older adults have revealed amplitude reductions, and sometimes peak latency delays in the ERN (Band & Kok, 2000; Falkenstein, Hoormann, & Hohnsbein, 2001; Mathalon, et al., 2003; Mathewson, Dywan, & Segalowitz, 2005; Nieuwenhuis, Ridderinkhof, Talsma, Coles, Holroyd, & Kok, 2002), the N450 (e.g., Mager, et al., 2007; West, 2004), and the conflict-related N2 components (Falkenstein, Hoormann, & Hohnsbein, 2002; Hämmerer, Li, Müller, & Lindenberger, 2010). These findings suggest that conflict monitoring efficiency is reduced in later adulthood. This interpretation is further supported by fMRI studies showing that older adults exhibit activation of ACC during both congruent and incongruent trials of the Stroop task, whereas the ACC is more selectively activated during incongruent trials for younger adults (e.g., Milham, et al., 2002). This finding suggests that the ACC responds less differentially to situations of high conflict, and thus is less reliable as a conflict monitoring mechanism in the elderly. More direct evidence that the ACC experiences functional decline in later adulthood is provided by an experiment showing that larger ACC volume is related to better Stroop performance in older adults (Elderkin-Thompson, Ballmaeir, Hellemann, Pham, & Kumar, 2008). Further neuroimaging studies have shown that aging is associated with ACC atrophy (e.g., Bergfield, et al., 2010; Good, et al., 2001; Mann, et al., 2011) and metabolic changes in ACC functioning (e.g., Pardo, et al., 2007).

To summarize the review thus far, the extant literature suggests that age differences in the ability to suppress pre-potent responses in cognitive control tasks is related to age-related losses in the integrity of conflict monitoring mechanisms supported by the ACC. However, it is yet unclear whether age-related declines in cognitive control on the behavioural level are also related to changes in response implementation. In the vast majority of cognitive control tasks used in the laboratory, behavioural responses come in the form of manual actions, such as button presses. The common observations of age-related declines in cognitive control are thus potentially confounded by known age-related changes in motor performance and control. One of the main concerns of the current dissertation is to explore the contributions of both cognitive and motor processes to cognitive control declines in later adulthood. To introduce this goal in more detail, I will first turn to a brief review of the literature on age-related changes in motor control.

1.7 Motor Control in later adulthood

Age-related declines in human motor performance and control are well documented (see Ketcham & Stelmach, 2001; Seidler, et al., 2010 for reviews). Aging comes with deficient motor functioning in terms of coordination difficulties (e.g., Heuninckx, Wenderoth, & Swinnen, 2008; Seidler, Alberts, & Stelmach, 2002), movement slowing (e.g., Hicks & Birren, 1970; Houx & Jolles, 1993), increased movement variability (e.g., Contreras-Vidal, Teulings, & Stelmach, 1998), and gait, posture, and balance disturbances (e.g., Kovacs, 2005; Scherder et al., 2007; Tang & Woollacott, 1997). It is clear from the literature that changes in the motor system of older adults affects both fine, and gross motor control. For example, declines in motor performance of older adults compared to younger adults have been documented in terms

of slower planning during aiming movements (e.g., Haaland, Harrington, & Grice, 1993), longer time to completion in mirror drawing tasks (e.g., Kennedy & Raz, 2005), and slower peak velocity in point-to-point reaching movements (e.g., Ketcham, Seidler, van Gemmert, & Stelmach, 2002). Age-related declines in fine motor performance have been observed in a variety of tasks, including, but not limited to, fine motor sequencing (e.g., Howard & Howard, 1989, 1992), dexterous manipulation of objects (e.g., Cole, Cook, Hynes, & Darling, 2009), rhythmic tapping (e.g., Krampe, Engbert, & Kliegl, 2002), and handwriting (e.g., Contreras-Vidal et al., 1998). This short, and selective review demonstrates that motor performance suffers with advancing age on a variety of tasks. The changes that occur in motor control in later adulthood are likely due in part to peripheral changes in muscle strength/elasticity, sensory receptor function, peripheral nerve function, joint dynamics, etc. However, recent interest has grown in exploring the contribution of central nervous system changes to motor performance in later adulthood (see Seidler, et al., 2010). That is, researchers have become more interested over the past few decades in the relationship between age-related changes in higher order cognitive processes such as attention and cognitive control, and motor performance.

1.8 Interdependence between cognitive and sensorimotor control in aging

Clearly there are significant age differences in motor performance, and motor control processes, and it is beyond the scope of this dissertation to review the evidence exhaustively. The main reason to introduce these ideas in the current discussion is to acknowledge that age-related declines in motor control likely contribute to age differences in behavioural measures of cognitive performance. This observation is certainly not novel. In fact, for some time researchers have explored the interaction

between cognitive and motor processes in later adulthood. One of the key observations from this literature is that there is an increase in the interdependence between cognitive and sensorimotor processes with advancing age. Such claims are made on the basis of cross-sectional and longitudinal studies demonstrating increased covariation among cognitive and sensorimotor performance in later adulthood (e.g., Anstey, Lord, & Williams, 1997; Li & Lindenberger, 2002; Lindenberger & Baltes, 1994). Experimental evidence demonstrating this interdependence between cognitive and motor processes in the elderly comes from the dual-task literature.

Dual-task paradigms are commonly used to assess the ability to divide attention between two concurrently performed tasks. The ability to divide limited cognitive resources between the two tasks is measured through the magnitude of dual task costs. That is, by measuring the reductions in accuracy and response latency when performing two tasks together, compared to performing the tasks in isolation. It is generally observed that older adults exhibit larger dual-task costs than younger adults in a range of cognitive tasks (see Verhaeghen & Cerella, 2002).

When applied to concurrent motor and cognitive tasks, the dual-task paradigm has revealed age differences in the pattern of dual-task costs associated with motor and cognitive performance during balance recovery tasks (e.g., Brauer, Woollacott, & Shumway-Cook, 2001), fine motor sequencing (e.g., Fraser, Li, & Penhune, 2010), walking (e.g., Kelly, Schrager, Price, Ferrucci, & Shumway-Cook, 2008; Li, Lindenberger, Freund, & Baltes, 2001), and other cognitive-motor task combinations. These studies demonstrate that motor tasks are more attentionally demanding in the elderly compared to younger adults. In fact, a large literature supports the idea that older

adults recruit cognitive control processes that are not necessary for younger adults to perform the same movement tasks (see Li & Lindenberger, 2002; Seidler, et al., 2010).

Age-related increases in the recruitment of cognitive processes for motor performance are commonly explained either as a de-differentiation of function, or as compensatory (see Seidler et al., 2010). The dedifferentiation account suggests that during childhood development cognitive functions become more distinct, or differentiate, whereas later in adult development cognitive functions become more closely related, or dedifferentiate (e.g., Anstey, Hofer, & Luszcz, 2003; Baltes & Lindenberger, 1997; de Frias, Lövdén, Lindenberger, & Nilsson, 2007). The key to the dedifferentiation hypothesis is that recruitment of cognitive functions for motor performance is not necessarily beneficial for older adults' behaviour; rather there are simply increased correlations among different cognitive measures. Thus, the recruitment is non-selective in nature, and represents a reduction in the specificity of individual cognitive processes, and an increase in inappropriate recruitment with advancing age. The alternative view is that older adults recruit additional cognitive resources, to compensate for age-related cognitive declines (e.g., Cabeza, 2002). For example, older adults may recruit cognitive processes to compensate for normal age-related declines in motor performance (e.g., Mattay, et al., 2002; Wu & Hallett, 2005). Regardless of whether this age-differential recruitment of cognitive processes for motor performance is compensatory, the fact remains that there is an increasing interdependence between cognitive and motor functions in later adulthood.

1.9 Using motor performance measures to study cognitive control

This age-related increase in the interdependence between cognitive and motor functions highlights the importance of determining how age differences in cognitive performance influence response implementation processes. With respect to the current interest in pre-potent response suppression, it is critical that we improve our understanding of how conflict monitoring, and cognitive control deficits relate to motor control processes involved in response implementation in the elderly. Although dual-task studies have revealed a great deal about the nature of changing cognitive-motor interactions in later adulthood, they may be less well suited to exploring the relationship between conflict monitoring, cognitive control, and motor control because of the high demands placed on the ability to divide attention. Taxing the attentional system by requiring older adults to perform more than one task at a time likely confounds our assessment of the influence of cognitive control on motor performance. An alternate approach that will more clearly reveal the nature of this relationship is to borrow from techniques for measuring motor performance, and use them to assess behaviour of older and younger adults on pre-potent response suppression tasks. In fact, a number of studies have used ERPs to measure a component related to motor preparation: the lateralized readiness potential (e.g., Band & Kok, 2000; Danek & Mordkoff, 2011; De Jong, Coles, & Logan, 1995; Ullsperger & von Cramon, 2001; Vallesi & Stuss, 2010; van Boxtel, et al., 2001; Zeef & Kok, 1993) to study pre-potent motor response suppression and cognitive control. Similarly, researchers have used electromyography (e.g., Szücs et al., 2009) to study muscle activity during response suppression. The majority of these studies have explored the ability to withhold a response either in a Go/No-go, or stop-signal task. These studies reveal a great deal about the mechanisms involved in detecting a conflict,

and interrupting the preparation of a pre-potent motor response. They also reveal important details about the nature of the response conflict experienced in such tasks. However, these studies reveal less about the influence of the conflict-control loop (Carter & van Veen, 2007) on movement production. This is an especially important question for aging research because of the above-mentioned increase in interdependence between cognitive and motor functions. To explore this issue, a handful of studies have explored movement kinematics during pre-potent response suppression tasks in the elderly (e.g., Potter & Grealy, 2008; Trewartha, Endo, Li, & Penhune, 2009). For example, Potter and Grealy (2008) used motion capture in order to track the movements of younger and older adults during a pre-potent movement inhibition task. Their results suggested that even when older adults successfully inhibited a response, they had difficulty controlling subsequent movements compared to younger adults. This finding suggests an age-associated disconnect between conflict detection, pre-potent response suppression, and movement control processes.

In order to assess the role of cognitive control processes in mediating conflict in motor response production we developed a motoric version of a pre-potent response task (Trewartha et al., 2009) that is a modified version of a serial reaction time task (Nissen & Bulemer, 1987). This task allowed us to manipulate the pre-potency of certain motor responses, and to present responses that conflicted with that pre-potent tendency. Specifically, we cued younger and older participants to respond to sequences of key presses with the four fingers of their right hands on four consecutive keys on a piano-type keyboard. While performing the task, we recorded the participants' movements using 3-D motion capture. The specific sequences were manipulated in order to generate a pre-

potent response tendency. Briefly, particular pairs of key presses were presented repeatedly in order to induce a pre-potent pair of key presses. Once this paired-association was learned, we presented participants with pairs of key presses that violated the pre-potent response expectancy. Those violation pairs were embedded within random sequences of key presses and were compared between the groups to explore age-related differences in response suppression and re-programming. To explore cognitive and motor contributions to overall RT, we decomposed each movement into planning and execution phases. The main finding was that in both age groups performance suffered on the conflicting responses relative to the pre-potent responses, indicating an interference effect. However, the interference effects were larger for older than younger adults. The movement data revealed that younger, but not older adults, shortened overall RT on conflict trials by executing the movement faster than the pre-potent responses. These data suggested that younger adults compensated for longer planning time during conflicts by executing the movements more quickly (Trewartha, et al., 2009). Older adults were less able to use conflicting information to trigger adjustments in movement control that would reduce the impact of the conflict on overall RT. These findings are consistent with the Potter and Grealy (2008) study, and with suggestions that the conflict-control loop is impaired in later adulthood. Although younger and older adults exhibited different movement patterns during pre-potent response suppression, some remaining questions motivated the current experiments. The first experiment explored whether or not there are conditions under which older adults movement patterns would be similar to that of younger adults. Specifically, if conflicting responses were presented more frequently, would older adults' pre-potent response suppression improve? The second experiment

sought to directly explore the nature of the interaction between conflict monitoring, cognitive control, and movement patterns of younger and older adults by exploring the neurophysiological correlates of those cognitive processes during pre-potent response suppression.

1.10 Current studies

The above literature review provides a theoretical background for the two empirical chapters in this dissertation (chapters 2 & 3). For both experiments we used modified versions of the multi-finger sequencing task that we used previously (Trewartha, et al., 2009). The details of those modifications will be saved for the individual chapters. The following is a brief introduction of the goals of these studies.

The first experiment was designed to explore the extent to which younger and older adults can improve in their ability to respond to conflict if it they are exposed to conflict more frequently (Trewartha, Penhune, & Li, 2011). The original conflict monitoring theory proposed that the functional role of a conflict detection mechanism is to trigger adjustments in cognitive control that can improve our performance on subsequent conflict trials (e.g., Botvinick, et al., 2001). This improvement is often referred to as conflict adaptation. Given the evidence, reviewed earlier, that older adults are impaired at monitoring for conflict it is important to determine to what extent they are able to adapt their performance during subsequent conflict trials. The question of whether older adults experience a similar conflict adaptation effect as younger adults has not been explored often in the literature. The limited findings are mixed, with some research showing that older and younger adults exhibit similar conflict adaptation effects (e.g., Mutter, Naylor, & Patterson, 2005; West & Moore, 2005), whereas others suggest that

older adults benefit less from frequent exposure to conflict (e.g., West & Baylis, 1998). Theoretically, if older adults experience diminished conflict monitoring, they should be less efficient at triggering adjustments in cognitive control than younger adults. The main goal of the first experiment in this dissertation is to determine if movement analyses can provide insight into the discrepancy in the literature concerning conflict adaptation effects in the elderly.

The first goal of the second experiment was to explore the neurophysiological correlates of conflict processing during conflicting response performance. To achieve this goal, we concurrently recorded EEG and motion capture data while participants performed the task. Using the ERP data, we tested the prediction that older adults would exhibit a diminished conflict-related N2 component, and that this age-related change in conflict monitoring would explain age differences in movement patterns. This experimental design allowed us to explore the time-course of conflict monitoring in relation to movement trajectories on conflicting, compared to pre-potent responses. The second goal of this experiment was to examine whether the context in which conflicting responses are encountered influences age differences in the movement patterns of younger and older adults. To this end, we combined the behavioural paradigms used in our previous experiments (Trewartha et al., 2009; Trewartha et al., 2011) to determine whether conflicting response performance would vary between the age groups if the conflicts were embedded within random sequences, or repeated pairs of responses. The novel contribution of these two experiments is to provide insight into age differences in the interaction between conflict monitoring and motor performance within a single task.

Chapter 2: Manuscript 1

Movement kinematics of pre-potent response suppression in aging: Effects of conflict salience and frequency

2.1 Abstract

Objectives

The purpose of the current study was to explore the role of adjustments in motor control and conflict adaptation in younger and older adults' pre-potent response suppression.

Methods

Participants performed repeated pairs of key-presses on a piano-type keyboard, as well as key-presses that conflicted with that pre-potent pair. We used motion capture to assess cognitive and motor contributions to conflicting responses presented once, twice, or three times within single trials.

Results

Older adults performed the first conflicting response in a series as well as young adults, but at a cost to pre-potent response performance. Younger adults improved performance with increased conflict frequency, whereas older adults did not. Older adults spent less time planning, and more time executing their conflicting responses, with the opposite pattern in younger adults.

Discussion

Overall, increasing the frequency of conflicting response presentation was detrimental to older, but not younger adults' pre-potent response performance. In addition the results indicate an age-related decline in conflict adaptation. The results are discussed in terms of current models of cognitive control.

2.2 Introduction

Cognitive control processes have been described as being responsible for the planning, coordinating, monitoring and sequencing of other cognitive operations (e.g., Salthouse, Atkinson, & Berish, 2003). In the laboratory cognitive control is often studied by asking participants to suppress pre-potent, or well-learned responses. Some tasks rely on responses that are pre-potent because of a habitual tendency to respond in a certain way, such as reading a word in the Stroop task (Stroop, 1935). Other pre-potent responses, like those in the Eriksen flanker task arise because of a perceptual-motor bias (Eriksen & Eriksen, 1974). Researchers can also create pre-potent responses by training participants to expect particular response requirements. For example, in the motor sequencing literature participants are trained to produce sequences of responses through repetition (see Koch, 2007). When over-learned, each response in the sequence acts as a cue for the next response in the sequence. Similarly, participants can be trained to associate individual pairs of key-presses through repetition. Completion of the first press in the associated pair becomes a prime for the pre-potent expectancy of the second press from that pair (Trewartha, Endo, Li, & Penhune, 2009). Generally, presenting a stimulus that is incongruent with a pre-potent response leads to increased error rates and/or reaction time.

In the cognitive aging literature, age-related deficits in pre-potent response suppression are observed across a broad range of tasks including the Stroop, stop signal (e.g., Pilar, Guerrini, Phillips, & Perfect, 2008), and Simon tasks (e.g., Van der Lubbe & Verleger, 2002). Theories to explain these age-related changes have been expressed in

terms of inhibitory control (e.g., Hasher, Zacks, & May, 1999), and conflict monitoring deficits (e.g., Braver & Barch 2002).

Regardless of the specific cognitive mechanisms that allow pre-potent response suppression, they must exert an influence on the motor control processes involved in executing the appropriate response. An important approach for exploring the nature of the relationship between cognitive processes and motor responses is to use kinematic analyses to delineate the contributions of movement preparation and execution to response suppression. For example, movements that are cued by a stimulus can be decomposed into meaningful components such as planning and execution phases. Planning is defined as the latency to begin executing a movement and represents stimulus identification, response selection, and movement preparation/programming, whereas execution is the time from movement initiation to termination and is sometimes referred to as movement time (e.g., Bosman, 1993). Explanations of age-related pre-potent response suppression deficits can benefit greatly from such analyses because there are known age differences in various kinematic measures of movement production (Ketcham & Stelmach, 2001; Haaland, Harrington, & Grice, 2003; Kennedy & Raz, 2005) that contribute to overall reaction time differences, and to the ability to adjust control of movements in response to changing task demands (Ketcham, Seidler, Van Gemmert, & Stelmach, 2002; Seidler, 2006).

The reduced ability of older adults to adjust movement parameters in response to changing task demands suggests that age-related cognitive changes influence motor control. In a recent experiment, we explored kinematic measures of pre-potent response suppression in younger and older adults (Trewartha et al., 2009). Participants were

trained to make pre-potent pairs of key-presses, and then were tested on violations of the pre-potent pair in which the second key-press conflicted with the expected response. These violations were embedded within a random sequence of key-presses, making them difficult to detect. Although pre-potent response suppression led to increased planning time on the conflicting responses for both age groups, the younger adults compensated by shortening the time spent executing those key-presses. Older adults had slower planning time and were unable to modify movement execution in the face of pre-potent response suppression. Thus, younger adults increased movement execution speed to successfully suppress pre-potent responses. It is unclear however, whether older adults' pre-potent response suppression deficit was due to deficiencies in conflict detection or in the ability to adjust movement parameters. Thus, the motivation for the current study was to shed light on this issue by reducing the need for participants to rely on conflict detection mechanisms. This was accomplished by embedding conflicting responses within strings of repeated key-press pairs, and by systematically varying the proportion of conflicting responses. In this context, any age-related differences in the pattern of planning and execution time during pre-potent response suppression would largely be attributable to motor control processes.

The effects of increased exposure to conflict have been explored using the flanker, (Gratton, Coles, & Donchin, 1992), Simon (Stürmer, Leuthold, Soetens, Schröter, & Sommer, 2002), and Stroop tasks (Kerns, Cohen, MacDonald, Cho, Stenger, & Carter, 2004), revealing that the interference effect is smaller on conflict trials that were preceded by other conflict trials. This finding has been referred to as the *Gratton effect*, or conflict-adaptation effect (e.g. Verbruggen, Notebaert, Liefooghe, &

Vandierendonck, 2006). These types of findings have motivated the development of the conflict monitoring theory of cognitive control (e.g., Botvinick, Braver, Barch, Carter & Cohen, 2001). Exploring conflict-adaptation effects in the elderly would help clarify the nature of age-related deficits in pre-potent response suppression. However, research on this topic has been relatively sparse. For younger adults increasing the proportion of congruent items in the Stroop task increases the interference effect. Put another way, if participants are more frequently exposed to conflict, the interference effect is reduced (e.g., Lowe & Mitterer, 1982). In the elderly, the limited studies are mixed with some evidence suggesting that older adults benefit less from increasing the proportion of incongruent trials (e.g., West & Baylis, 1998) but other research showing evidence of age equivalence in conflict adaptation (e.g, Mutter, Naylor, & Patterson, 2005; West & Moore, 2005). These inconsistencies in the literature highlight the need to use alternative paradigms to explore the general effects of increasing exposure to conflict on cognitive control in the elderly, and provide motivation for delineating cognitive and motor contributions to conflict adaptation. To this end we modified our previous paradigm (Trewartha et al, 2009) to test whether repeated exposure to conflict changes the relative proportion of time spent planning and executing conflicting responses in young or elderly participants.

In the current study we embedded conflicting responses within strings of repeated pairs of key-presses rather than random sequences. This modification effectively reduced the complexity of the task such that there were only two possible responses in each series: a pre-potent, well-learned pair, or a conflicting pair. We reasoned that this would reduce the demands placed on the conflict monitoring system allowing us to isolate age-

related differences in movement planning and execution during pre-potent response suppression. Secondly, we explored whether manipulating the frequency with which participants encountered conflict would affect their ability to adjust movement execution parameters. We manipulated conflict frequency by including one, two, or three conflicting key-presses within each 10-key-press conflict trial. Consistent with a conflict-adaptation effect, it was predicted that participants would perform better with repeated exposure to conflicting key-presses within a trial. Finally, we predicted that the decreased need for conflict detection mechanisms, combined with increased exposure to conflicting responses, would equally affect older and younger adults' performance.

2.3 Method

2.3.1 Participants

Twenty younger (19-36 years old, $M = 24.95$, $SD = 5.21$), and 20 older adults (60-75 years old, $M = 68.2$, $SD = 4.72$) gave informed consent to participate in this study, which was approved by Concordia University's Human Research Ethics Committee. Participants were right-handed, free from physical and neurological conditions affecting finger or hand movements, had less than three years of musical experience, and had not been practicing in the past 10 years. Each participant completed four neuropsychological tests: the WAIS Digit Symbol Substitution (Wechsler, 1981), the Extended Range Vocabulary test (ERVT, Form V2; Educational Testing Service, 1976), the Halstead-Reitan Trail Making Test, parts A and B (Reitan, 2001) and the Stroop test (Adapted from Spreen & Strauss, 2001). All participants performed as expected for their age group based on previous literature (Table 2.1).

Table 2.1

Means and Standard Errors of the Neuropsychological Tests and the t-test Results of the Age Group Comparisons for Each Test.

Neuropsychological Test	YA	OA
WAIS Digit Symbol**	87.40 (4.31)	71.70 (3.79)
ERVT*	9.24 (1.09)	12.28 (0.90)
Trails Difference Scores**	24.60 (3.40)	49.75 (6.99)
Stroop Interference Score*	0.394 (0.03)	0.670 (0.13)

Note: Mean scores are presented with standard error in parentheses for the number of items completed (max. 133) in 2 minutes on the WAIS (Weschler Adult Intelligence Scale) Digit Symbol Substitution subtest, the number of correct items, with a penalty for errors, on the Extended Range Vocabulary Test (ERVT), the difference in time (s) to complete versions B and A of the Trail Making test (Trails), and the difference between the seconds per item completed on the Congruent and Incongruent versions of the colour Stroop test. * $p < .05$, ** $p < .01$.

2.3.2 Apparatus

Participants made sequences of key-presses using the four fingers of their right hand on a piano-type keyboard while seated in front of a 17" flat screen monitor. Four dark-grey, 3" x 3" boxes oriented horizontally on the screen represented each of their fingers in a left-to-right manner. Each box, and finger, also corresponded to one of four consecutive keys on the keyboard on which pieces of Velcro were affixed to act as tactile cues to aid participants in remaining on the correct keys (see Figure 2.1). The boxes on the screen changed color one at a time to cue which finger/key the participant should press. The keyboard measured accuracy whereas a 3-D motion capture system (VZ3000; Phoenix Technologies Inc., Burnaby, BC, Canada) obtained the movement data. The stimulus presentation software was custom written in C# on version 1.1 of the Microsoft .NET Framework and also collected timing data of the motion capture frames and stimulus presentation for offline synchronization.

2.3.3 Procedures

Participants performed 10-key-press trials without performance feedback. The task instructions were to follow along as each box lit up and press all the way down on the corresponding key with the corresponding finger as quickly and accurately as possible. Stimulus duration was 400 ms, with a 400 ms inter-stimulus interval (ISI), and a 3000 ms pause between each trial. Participants performed three conditions: the first was a block of 6 random sequences using all four fingers that acted as a baseline of the ability to react to and follow along with the stimuli. The second condition was a homogeneous "repeated only" condition in which 15 trials were presented involving the repetition of

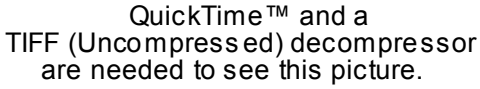


Figure 2.1. Illustration of the computer/keyboard set-up for the motor task (Top panel). Participants placed each of the four fingers of their right hand on Velcro pads affixed to four consecutive keys on the keyboard. One LED marker was placed on each fingernail of the right hand, and nine motion capture cameras were oriented in a semi-circle around the computer/keyboard set-up. Numbers on the keys are for illustration purposes only. The table (bottom panel) presents examples of the sequences used in each experimental condition.

the same pair of key-presses five times in every trial. This induced a pre-potent pair of key-presses that could be used to create conflicting pairs in subsequent blocks. The final condition consisted of nine heterogeneous blocks of 20 trials each that contained both repeated only, and conflict trials (see Figure 2.1 for examples). There were a total of 120 repeated only trials in these blocks that were identical to those in homogeneous condition except that they occurred in blocks also containing conflict trials. The 60 remaining trials were conflict trials. Each conflict trial included a conflicting key-press pair consisting of the first press of the repeated pair, followed by an unexpected alternate second key-press. These conflicts were embedded within trials of repeated pairs and conflict frequency was manipulated by including one, two, or three conflicts in each trial. There were 20 trials of each conflict frequency randomly dispersed among the nine heterogeneous blocks with the constraint that each conflict trial would be separated by one, two, or three repeated only trials. The serial position of the conflicts within each trial was also randomized to ensure that the locations of conflicting responses were not predictable. The particular key-press combination that was used as the pre-potent pair was counterbalanced across participants.

2.3.4 Data Analyses

The data were separated into the following key-press pairs: a) random, b) repeated only in the homogeneous condition, c) repeated only in the heterogeneous condition, d) repeated responses within conflict trials, and e) conflicting key-presses; separated into one, two, or three conflicts. The dependent variables were calculated only for the second key-press in each pair as the first key-press acted as the prime for the pre-potent response. For the random sequences all key-presses were included.

A response was considered accurate if the correct key was pressed while the stimulus was on the screen or within the ISI. Planning and execution time were calculated on unfiltered data using analysis tools developed in Matlab 2008b (described by Trewartha et al., 2009). Briefly, full key-presses were identified as local minima (i.e., troughs) among samples that were more than two standard deviations below the baseline in the vertical (z) dimension. Movement initiation was calculated using a backward search for the point at which the slope was greater than -0.05 mm/ms for each key-press. The amount of time from stimulus presentation to movement initiation was defined as the planning time, whereas the time from movement initiation to the trough defined execution time (Figure 2.2). Together the kinematic measures provide an estimate of reaction time, and are only presented for correct responses. For all three dependent measures, key-press types were averaged across trials within participant, and across participants within age groups for comparison[1].

2.4 Results

2.4.1 Overall Conflict Effects

To explore the overall effects of exposure to conflict younger and older adults' performance was compared on the seven different response types: random, repeated only homogeneous, repeated only heterogeneous, repeated with conflict, and conflicting responses in 1, 2, and 3-conflict trials. Each dependent measure was subjected to a 2 (age group) x 7 (response type) ANOVA.

[1] Due to the frequency of conflict manipulation there are more data points for the repeated responses than the conflicting responses. To test whether the unequal number of data points affected the results, all analyses were conducted a second time using a random sub-set of the repeated responses to equate the number of data points in each condition. There were no changes in the pattern of effects for any of the analyses. In the interest of including the full data, results are presented from the first analysis.

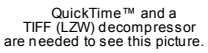


Figure 2.2. Illustration of the parsing of a single key press into the kinematic time-course variables of planning and execution time.

For accuracy (top panel of Figure 2.3) this overall ANOVA revealed significant main effects of response type, $F(6,33) = 14.24$, $p < .001$, $\eta_p^2 = 0.73$, and age group, $F(1,38) = 4.3$, $p < .05$, $\eta_p^2 = 0.10$, and a significant interaction between age group and response type, $F(6,33) = 3.15$, $p < .05$, $\eta_p^2 = 0.37$. Likewise, in planning time (center panel of Figure 2.3) there were significant main effects of response type, $F(6,33) = 22.65$, $p < .001$, $\eta_p^2 = 0.84$, and age group, $F(1,38) = 4.38$, $p < .05$, $\eta_p^2 = 0.12$, and a significant

interaction between age group and response type, $F(6,33) = 3.31$, $p < .05$, $\eta_p^2 = 0.42$. Finally, for execution time (bottom panel of Figure 2.3) there was a significant main effect of age group, $F(1,38) = 4.43$, $p < .05$, $\eta_p^2 = 0.12$, and a significant interaction between age group and response type, $F(6,33) = 4.07$, $p < .01$, $\eta_p^2 = 0.46$, but no main effect of response type ($p > 0.32$). In order to explore these interactions, pair-wise comparisons were conducted using a Bonferroni correction for each dependent variable.

First, in the homogeneous block, younger adults were better able to respond to a series of random key-presses than older adults in terms of accuracy, $t(19) = 3.17$, $p < 0.01$, and had shorter planning time, $t(19) = 3.91$, $p < 0.001$, but execution time did not differ between the groups ($p > 0.27$). Importantly, there were no differences between the age groups for the repeated only homogeneous responses on any of the dependent measures (all $p > 0.52$). Thus, despite age differences in performance of random sequences of key presses, age-equivalence was observed for performance of the pre-potent responses (left side of each panel in Figure 2.3). With this in mind, comparisons were made among the repeated and conflicting responses in the heterogeneous blocks.

In order to assess the global effect of introducing conflicting responses in the heterogeneous blocks, within group comparisons were made between the repeated only responses in the homogeneous and heterogeneous conditions. Younger adults did not exhibit a difference for any of the dependent measures for this comparison (all $p > 0.25$), nor did the older adults (all $p > 0.95$). However, it appears from the center panel of Figure 2.3 that planning time differed between the groups for the repeated responses in the heterogeneous condition.

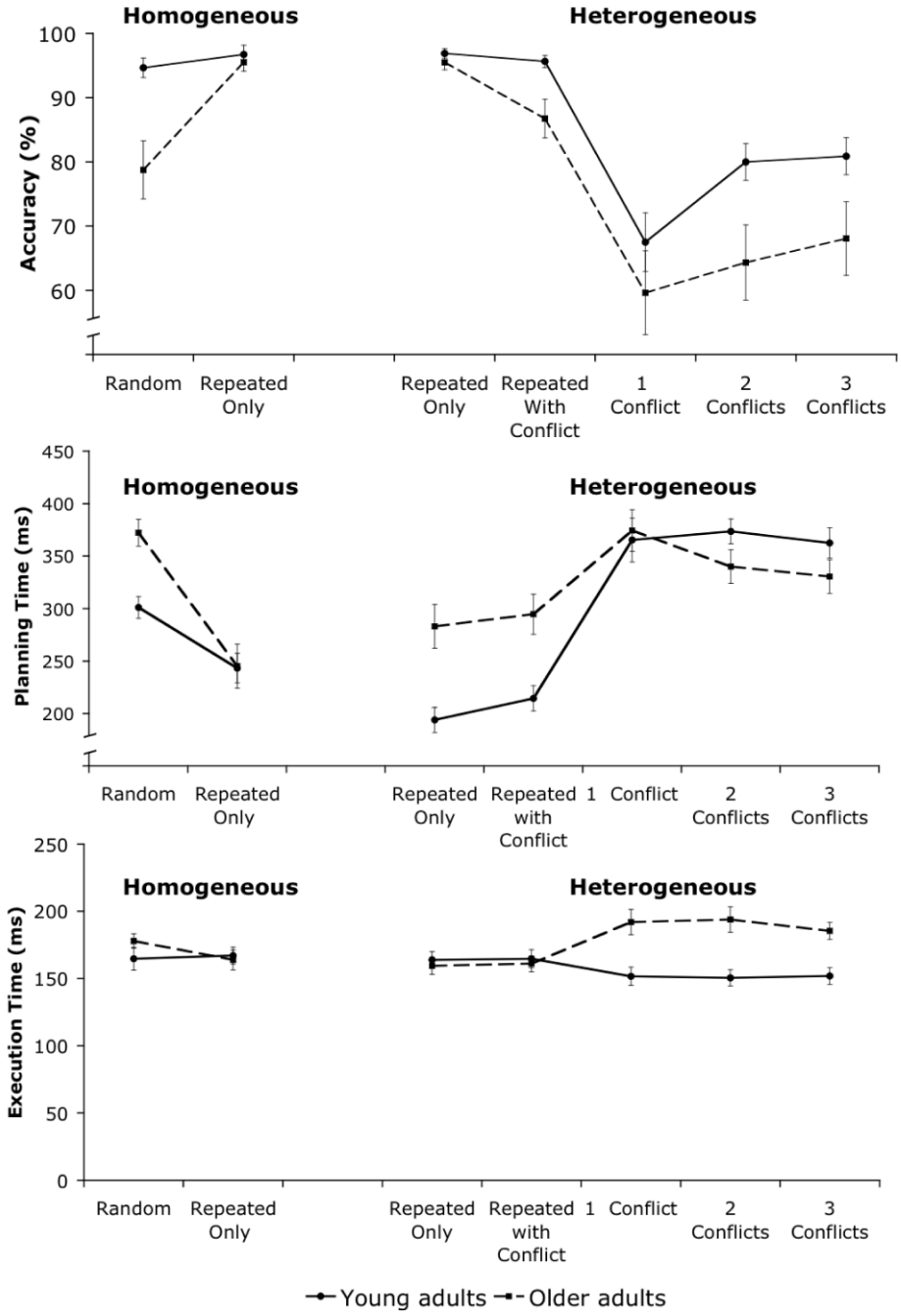


Figure 2.3. Younger and older adults' behavioral data in the homogeneous and heterogeneous conditions. Averages are shown for all seven response types: random, repeated only homogeneous, repeated only heterogeneous, repeated with conflict, and conflicting responses averaged within 1-, 2-, and 3-conflict trials. Panel (a) displays averaged accuracy, (b) displays averaged planning time, and (c) displays execution time. Error bars represent standard error of the mean.

A follow-up, between-groups comparison of the repeated only responses in the heterogeneous condition confirmed that older adults had longer planning time than younger adults, $t(19) = 3.31$, $p < 0.01$. Thus, the introduction of conflict trials in the heterogeneous condition compromised the age-equivalence in pre-potent response performance observed in the homogeneous block.

In order to assess the more local effects of responding to pre-potent responses within conflict trials, repeated only responses in the heterogeneous condition were compared to repeated responses in conflict trials within-groups. Younger adults did not differ for these response types (all $p > 0.25$), whereas older adults were less accurate, $t(19) = 6.33$, $p < 0.001$, and spent more time planning, $t(19) = -4.47$, $p < 0.01$, repeated responses that occurred within conflict trials. No other comparisons were significant (all $p > 0.95$). This suggests that in addition to the global effect of conflict, older adults experienced greater local costs than younger adults on repeated responses in conflict trials.

Finally, within-group comparisons were made to explore conflicting response performance across different levels of conflict (averaged within 1-, 2-, and 3-conflict trials) and with repeated only responses in the heterogeneous blocks (see right side of all panels in Figure 2.3). Overall, younger adults were less accurate for all levels of conflict relative to their repeated only responses ($t(19) = 6.56$, $p < 0.001$, $t(19) = 5.23$, $p < 0.001$, and $t(19) = 5.10$, $p < 0.001$, respectively). They also spent more time planning the conflicting responses ($t(19) = -6.6$, $p < 0.001$, $t(19) = -8.79$, $p < 0.001$, and $t(19) = -8.49$, $p < 0.001$, respectively), but showed no differences in execution time (all $p > 0.64$). Older adults showed the same pattern of lower accuracy for all levels of conflict ($t(19) = -6.82$,

$p < 0.001$, $t(19) = -7.94$, $p < 0.001$, and $t(19) = -7.09$, $p < 0.001$, respectively), and their planning time was longer, compared to their repeated only responses ($t(19) = -4.21$, $p < 0.01$, $t(19) = -3.66$, $p < 0.05$, and $t(19) = -3.30$, $p < 0.05$, respectively). However, the older adults also took longer to execute conflicting responses in all three trial types compared to their repeated only responses ($t(19) = -4.49$, $p < 0.01$, $t(19) = -4.20$, $p < 0.01$, and $t(19) = -4.18$, $p < 0.01$, respectively). This pattern differed from the younger adults who did not differ in execution time for conflicting and repeated responses. In addition, comparisons among the levels of conflict revealed that younger adults improved their accuracy in 2- and 3-conflict trials compared to 1-conflict trials ($t(19) = 4.31$, $p < 0.01$, and $t(19) = 4.47$, $p < 0.01$, respectively). No other comparisons were significant (all $p > 0.18$), indicating that older adults did not improve conflicting response performance in trials with more than one conflict.

To summarize, despite age equivalence in performing pre-potent responses in isolation, younger and older adults' performance differed on the repeated responses in the context of conflicting responses. For older adults only, conflicting responses interfered with performance on the repeated responses, both globally in the heterogeneous blocks, as well as locally on the repeated responses within conflict trials. Moreover, although both groups performed worse on conflicting responses than pre-potent responses, only younger adults improved their performance when more than one conflict was presented.

2.4.2 Conflict Adaptation

The improvement in younger adults' performance during trials with more than one conflict is consistent with a conflict adaptation effect. However, an alternative explanation is that the improvement was due to increases in the proportion of conflicting

responses within conflict trials. A genuine conflict adaptation effect would be observed if participants' performance improved on conflicting responses that were preceded by previous conflicting responses within a trial. We explored this by comparing the conflicting responses in terms of their position within each type of conflict trial (Figure 2.4) unlike the previous analysis in which we averaged across conflicts in each trial. Conflicts were separated into the following response types: one-conflict only, first and second conflict in a two-conflict trial, and first, second, and third conflict in a three-conflict trial. Each dependent variable was compared using a 2 (age group) x 6 (conflict position) ANOVA. For accuracy there was a significant main effect of response type, $F(5,34) = 11.64$, $p < .001$, $\eta_p^2 = 0.24$, and a significant interaction between age group and response type, $F(5,34) = 7.61$, $p < .001$, $\eta_p^2 = 0.17$, but no main effect of age group ($p > 0.07$). For planning time there were significant main effects of response type, $F(5,34) = 5.32$, $p = .001$, $\eta_p^2 = 0.45$, and age group, $F(1,38) = 4.11$, $p = .05$, $\eta_p^2 = 0.10$, and a significant interaction between age group and response type, $F(5,34) = 2.74$, $p < .05$, $\eta_p^2 = 0.30$. There was also a significant main effect of age in execution time such that older adults spent more time executing conflicting responses than younger adults, $F(1,38) = 18.57$, $p < .001$, $\eta_p^2 = 0.34$, but no other effects were significant (all $p > 0.67$).

Pair-wise comparisons revealed a conflict adaptation effect in the 3-conflict trials for younger adults as they were significantly more accurate on the second and third conflicting response compared to the first, $t(19) = -5.95$, $p < .001$, and $t(19) = -4.48$, $p = .001$, respectively (right side of top panel in Figure 2.4).

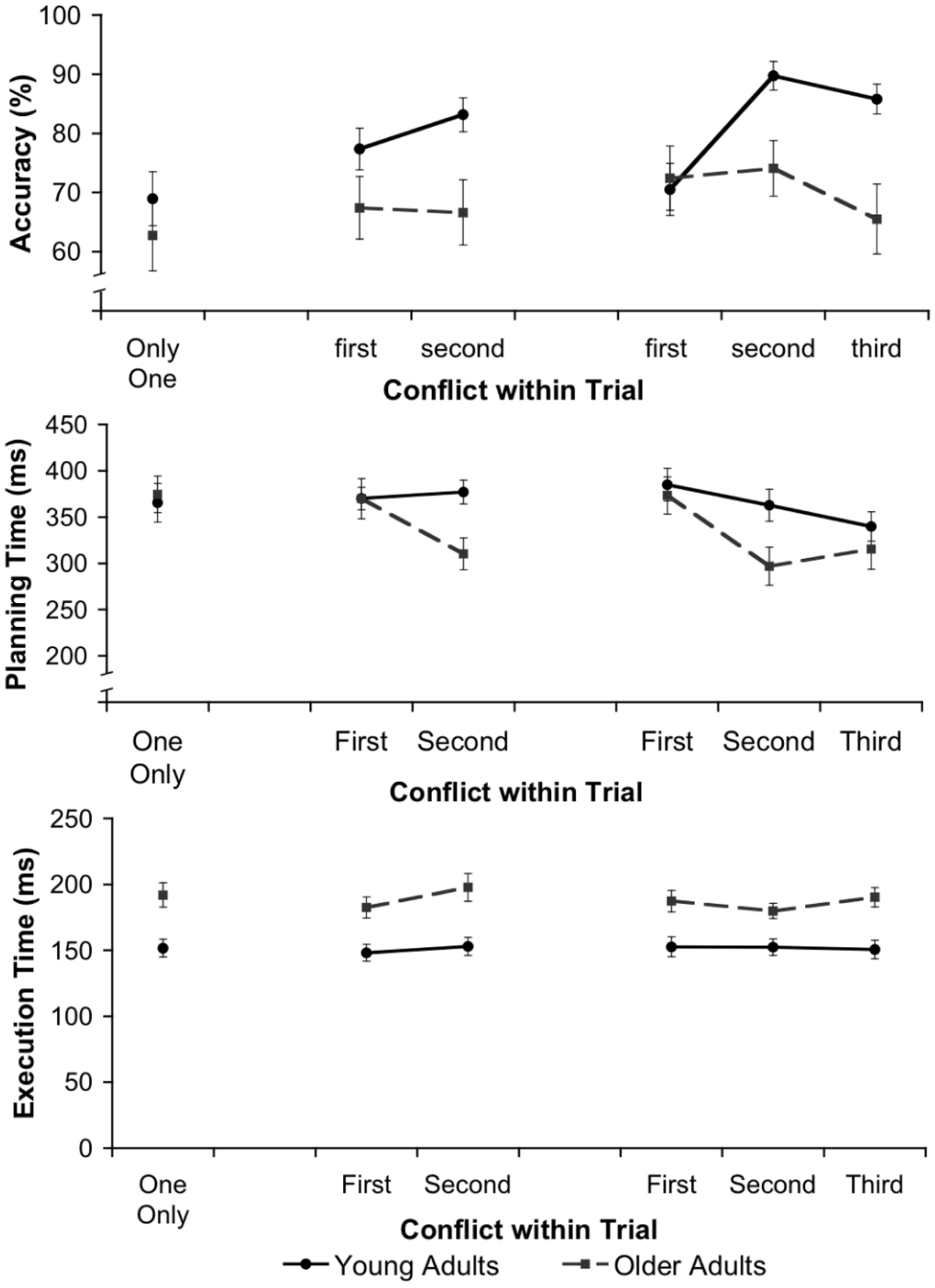


Figure 2.4. Conflict Frequency Data: younger and older adults' keyboard and motion capture data for six different conflict positions. Namely, conflicting responses in the one-conflict trials, first and second conflicts in the two-conflict trials, and the first, second and third conflict in the three-conflict trials. Panel (a) displays averaged accuracy, panel (b) displays averaged planning time, and (c) displays execution time. Error bars represent standard error of the mean.

No other comparisons were significant for the younger adults (all $p > .065$). Older adults did not improve in accuracy on subsequent conflicts within trials, rather they were marginally less accurate on the third conflict in a three-conflict trial compared to the second, $t(19) = -3.12$, $p = .053$ (no other comparisons reached significance, all $p > .09$). Interestingly, in the two-conflict trials older adults decreased planning time on the second conflicting response compared to the first, $t(19) = 3.40$, $p < .05$ (center of middle panel in Figure 2.4). Likewise, they decreased planning time on the second conflict in the three-conflict trial, $t(19) = 5.22$, $p < .001$, and marginally on the third, compared to the first conflict, $t(19) = 3.11$, $p = .055$ (right side of middle panel in Figure 2.4). No other comparisons were significant (all $p > .44$).

These analyses confirm that a conflict adaptation effect could account for improved accuracy of younger adults on trials with more than one conflict. Older adults did not improve in accuracy on the second or third conflict within a trial suggesting an age-related decline in the ability to benefit from previous exposure to conflict.

2.5 Discussion

The goal of this study was to isolate the role of conflict adaptation from conflict detection processes in age-related pre-potent response suppression deficits. To this end we minimized the need for conflict detection by embedding conflicting key-presses in series of repeated pairs, and manipulated the number of conflicts within each series. Two sets of findings emerged. First, although older adults performed conflicting key-presses as well as younger adults, their performance suffered on the pre-potent responses. Moreover, on the conflicting responses older adults exhibited shorter planning and longer

execution times, whereas younger adults showed the opposite pattern. Second, the more fine-grained analyses of conflict frequency effects revealed that age-equivalence in performance of a conflicting response was limited to the first conflict in a trial. Contrary to our prediction, only the younger adults improved performance with repeated exposure to response conflict. In fact, older adults became less accurate with repeated response conflict, and showed reductions in planning time. Although reducing the need to rely on conflict detection allowed older adults to perform as well as young adults on the first conflict in a trial (c.f., Trewartha et al., 2009), they failed to show a conflict adaptation effect for subsequent conflicts. Additionally, impaired performance on the pre-potent responses suggests that even when conflict detection demands were minimized older adults had difficulty regulating performance in response to changes in task context.

The finding that older adults were able to suppress the pre-potent response during the first conflict in a series is consistent with observations that increased conflict saliency can benefit older adults' performance in the Stroop task (e.g., Borella, et al., 2009). In contrast, our previous experiment revealed that older adults exhibited pre-potent response suppression deficits when conflicts were embedded within random sequences – a context in which conflict detection is challenging (Trewartha et al., 2009).

A possible explanation for this discrepancy is that the current paradigm has only two competing mental sets (i.e., the pre-potent response, or any conflicting response). In our previous experiment there were at least three mental sets because pre-potent and conflicting responses were performed within random sequences. In the task switching literature, global set-selection costs in reaction time, obtained by comparing blocks of task switching to blocks without switching, are often larger in older adults than local

costs of switching tasks (e.g., Mayr, 2001). Consistent with this, we observed age equivalence on the first conflicting pair in a series, which represents a local switch from performing the pre-potent pair. Additionally, global costs were only evident for older adults as their pre-potent response performance was reduced in the heterogeneous, compared to the homogeneous condition in which no mental set switch was required. Similar age differences in performance have been observed in the context of increased response choices (e.g., McDowd & Craik 1988), and multiple stimulus-response mappings (Kolev, Falkenstein, & Yardonova, 2006).

An alternative explanation of the difference between the current findings and those of Trewartha et al. (2009) is that older adults benefited from greater conflict awareness induced by embedding conflicts within repeated pairs, rather than random key-presses. Neurophysiological studies have dissociated mechanisms associated with conflict detection from those associated with conflict awareness (O'Connell, Dockree, Bellgrove, Kelly, Hester et al., 2007). There is evidence that the amplitude of ERP components associated with both detection and awareness are reduced in later adulthood (e.g., Band & Kok, 2000; Matthewson, Dywan, & Segalowitz, 2005; cf., Mathalon, Bennet, Askari, Gray, Rosenbloom, & Ford, 2005). In the current study, conflict detection demands are minimal, so preserved conflict awareness could account for older adults' pre-potent response suppression during the first conflict in a trial.

Despite improvements in performance on the first conflict in a series, older adults' performance suffered on the repeated responses in the heterogeneous condition, consistent with evidence of age-related declines in interference resolution (e.g., Rekkas, 2006). Moreover, the current data revealed that older adults failed to adapt their

performance based on previous exposure to conflict within trials. The conflict monitoring hypothesis (Botvinick et al., 2001) predicts that encountering conflicts should trigger adjustments in cognitive control aimed at reducing the effects of future conflicts. Support for this prediction comes in the form of behavioural improvements during subsequent conflict (Gratton et al., 1992; Stürmer et al., 2002), and changes in neural activity associated with those behavioural improvements (e.g., Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003; Kerns et al., 2004). Given these findings, and evidence of preserved conflict adaptation in the elderly (e.g., Mutter et al., 2005), we predicted that younger and older adults would improve with repeated exposure to conflict. We found support for conflict adaptation effects in younger adults' response selection accuracy, as error rates were reduced during the second and third presentation of a conflict in each trial.

However, contrary to our prediction, the older adults' accuracy worsened across subsequent conflicts. In fact, they only performed as well as younger adults on the first presentation of conflict in a trial. In addition, they shortened planning time on the second and third presentation of a conflict compared to the first presentation in a trial, but this did not benefit their overall performance. Shortened planning time, in the context of longer execution time, is consistent with evidence that older adults fail to inhibit pre-potent responses and must rather rely on online movement corrections (Potter & Grealy, 2006). This pattern differs from our previous finding that older adults spent more time planning conflicting responses than younger adults (Trewartha et al., 2009). This is likely because our previous paradigm required participants to rely on conflict detection mechanisms that are less efficient in later adulthood (Nieuwenhuis et al., 2002). In the

Potter and Grealy (2006), and our current study, conflict detection demands were minimized by only including responses that were either pre-potent, or conflicting. Given the speeded nature of these tasks, shorter planning time by older adults may reflect an impulsive response style due to uncertainty in mental set selection.

Overall, our findings are consistent with evidence of age differences in proportion congruent effects in the Stroop task (West & Baylis, 1998; cf., Mutter et al., 2005), suggesting that conflict adaptation in our paradigm may rely on similar mechanisms. Likely the pre-potent responses in our paradigm are less well-learned, and thus more susceptible to interference than the pre-potent responses in a Stroop task. Nevertheless, younger adults maintained pre-potent response performance while also showing a robust conflict adaptation effect. Older adults had more difficulty maintaining the pre-potent response representation during a condition in which it must also be suppressed.

The age-related performance decline across repeated conflicts may also be explained in terms of a deficiency in managing competing mental sets (e.g., Mayr & Liebscher, 2001), and is consistent with evidence that older adults exhibit a deficiency in adjusting cognitive control (e.g., Nessler, Friedman, Johnson, & Bersick, 2007). Such an age-related deficiency could be explained in the context of the dual mechanisms of control (DMC) account (Braver, Gray, & Burgess, 2007). This theory proposes that cognitive control is accomplished by both proactive anticipatory biasing of attention prior to stimulus presentation, and reactive, stimulus-driven adjustments in control. In the current study, participants may have maintained a mental set of the pre-potent response, and upon encountering the first conflict in a trial, used stimulus-driven reactive control to respond accurately. The observation of age invariance of the first conflict in a series is

consistent with evidence of preserved reactive control in later adulthood (see Braver et al., 2007). The initial exposure to the first conflict in a series could update working memory with an additional mental set (i.e., a conflicting response), and the interference introduced by proactively maintaining more than one anticipatory bias in working memory could burden older adults' ability to rely on proactive control. The fact that older adults failed to benefit from repeated exposure to conflict is consistent with proactive control deficits in later adulthood (see Braver et al., 2007). Thus, the current data are consistent with the idea that an age-related deficit in maintaining more than one mental representation in working memory may be exacerbated when participants frequently shift between mental sets.

In summary, under conditions of high conflict saliency older adults can perform conflicting responses as well as young adults, but only for the first conflict in a series. This is potentially due to a preservation of a reactive mode of cognitive control in later adulthood. However, in contrast to younger adults, increasing conflict frequency, rather than benefiting older adults' performance, exacerbates the interference between the well-learned and conflicting representations. Moreover, older adults' performance suffered on the pre-potent response in the heterogeneous condition where participants must frequently switch between pre-potent and conflicting responses. Interference between the proactive anticipation of the pre-potent response and a conflicting response led to age-related performance declines. Therefore, the current study provides evidence that declines in the ability to simultaneously regulate more than one mental representation could contribute to reduced conflict adaptation in later adulthood.

Chapter 3

Age differences in pre-potent response suppression investigated using concurrent motion capture and event-related potential recordings

3.1 Abstract

Objectives

The current study investigated the relationship between conflict monitoring and movement adaptation during pre-potent response suppression in aging through concurrent acquisition of motion capture and event-related potential data. We also explored the effects of task context on behavioural and ERP correlates of conflict monitoring.

Methods

Participants performed a motor sequencing task on a piano-type keyboard that included pre-potent pairs of key presses, and pairs that conflicted with the pre-potent response. Conflicts were embedded in random sequences (Conflict-in-Random), and repeated pre-potent responses (Conflict-in-Repeated) in order to assess context effects. The role of conflict monitoring was assessed by the conflict-related N2 ERP component.

Results

Aging was associated with reduced conflicting response performance in both conditions, with an exacerbated age effect when conflicts were embedded in repeated pairs. Younger adults demonstrated a fronto-central N2 component that correlated with movement adaptation during Conflict-in-Repeated responses. Older adults exhibited a diminished N2 that did not correlate with behavior. However, a subset of older adults who did adapt movement execution speed presented an N2 similar to that of the younger participants.

Discussion

Overall, the behavioural and ERP data revealed that older adults are impaired in utilizing conflict monitoring to support cognitive control over movement production. The results are discussed in terms of current theories of cognitive control and aging.

3.2 Introduction

The ability of older adults to manage various types of stimulus and response conflict has been an important topic in the past few decades. Those abilities are often thought to be at the heart of observed age-related declines in cognitive control that have been a common theme in the cognitive neuroscience of aging. Typically older adults perform worse than younger adults on tasks that require conflict processing (e.g., Stroop task). Recent findings have led to the speculation that this performance decline is related not only to less efficient conflict monitoring mechanisms, but also to age-related difficulties flexibly adapting movement execution during tasks requiring cognitive control (e.g., Trewartha, Endo, Li, & Penhune, 2009; Trewartha, Penhune, & Li, 2011). The current study was designed to test this suggestion directly by using concurrent motion capture and electroencephalogram recordings to explore both the kinematic and neural basis of performance in a pre-potent response task.

3.2.1 Cognitive Control and Conflict Monitoring in Aging

The concept of cognitive control refers to the ability to plan, organize and monitor other cognitive operations through the allocation of cognitive resources. A variety of experimental paradigms have been used to investigate cognitive control, including the Stroop (Stroop, 1935), Eriksen Flanker (Eriksen & Eriksen, 1974), Simon (Simon & Rudell, 1967), Stop-signal (Logan & Cowan, 1984), and Go/Nogo (Donders, 1868/1969) tasks. The common element to these tasks is the need to overcome an existing pre-potent response. For example, in the Stroop task one must overcome the pre-potent tendency to read a word (e.g., RED) in order to correctly indicate the color in which is printed (e.g., blue). A pre-potent response can be defined simply as any stimulus-response, or

response-response association that has been well learned through repetition such that it becomes an automatic response tendency. The need to overcome that automatic tendency requires cognitive control because conflict is introduced between the required, and pre-potent responses. One theory of cognitive control purports that encountering conflict, either in the stimulus or the response, triggers an increase in cognitive control aimed at reducing that conflict (Botvinick, Braver, Barch, Carter & Cohen, 2001). Thus, in tasks that require the suppression of a pre-potent response successful performance is dependent on initial detection of the conflict that will trigger increased cognitive control.

A common observation in the cognitive aging literature is that older adults are slower, and make more errors when attempting to overcome a pre-potent response compared to younger adults (see Braver & West, 2008 for a review). It has been argued that the age-related declines in pre-potent response suppression are due to conflict monitoring deficits in later adulthood (e.g., Braver & Barch, 2002). That is, older adults' performance suffers on pre-potent response tasks in part because of less efficient conflict processing that leads to a failure to trigger adjustments in cognitive control.

3.2.2 Neural Basis of Conflict Monitoring

Further support for the conflict monitoring deficit hypothesis of aging comes from the neuroimaging literature. Electrophysiological correlates of conflict monitoring are found in a number of event-related potential (ERP) components that are robustly observed following conflict. In terms of stimulus conflict, the most common components are the conflict-related N2 and N450. The N2 is a negative deflection in the ERP that peaks between 200-350 ms after stimulus presentation (Folstein & Van Petten, 2008; Nieuwenhuis, Yeung, Van Den Wlidenberg, Ridderinkhof, 2003; Yeung, Botvinick, &

Cohen, 2004; Yeung & Cohen, 2006). The N2 has been observed following stimulus presentation in a variety of pre-potent response tasks including the Go/Nogo task (e.g., Falkenstein, Hoormann, & Hohnsbein, 1999), the Flanker task (e.g., Yeung, et al., 2004) and the stop-signal paradigm (e.g., van Boxtel, van der Molen, Jennings & Brunia, 2001). Although there is evidence that there may be a variety of dissociable N2 components that differ in functional significance and topography, the conflict-related N2 is most often observed at anterior fronto-central electrode sites (see Folstein & Van Petten, 2008). The N450 is usually observed as a negative deflection that occurs approximately 300-500ms after the presentation of a conflicting stimulus in the Stroop task (West, 2003), and is also observed over fronto-central sites.

A number of studies using source localization techniques with ERP have shown these conflict-related components to be generated by the anterior cingulate cortex (ACC) and this conclusion has been corroborated by fMRI studies (for review see Botvinick, et al., 2004). The ACC has also been suggested as the neural generator of neurophysiological correlates of response conflict detection. Specifically, response-locked, fronto-central ERP components: the error-related negativity (ERN) and the error positivity (Pe) have been observed following the commission of errors. These various stimulus and response conflict related ERP components have motivated the theory that the ACC represents a general conflict monitoring system that ultimately triggers increased cognitive control through connections with the prefrontal cortex (PFC; see Botvinick, et al., 2004; De Pisapia & Braver, 2006).

Support for the notion that conflict monitoring deficits play a role in diminished cognitive control in later adulthood comes from observations that older adults exhibit

reduced amplitude in the ERN (Band & Kok, 2000; Falkenstein, Hoormann, & Hohnsbein, 2001; Nieuwenhuis, Ridderinkhof, Talsma, Coles, Holroyd, & Kok, 2002). Similar findings have been observed for stimulus-related conflict in the form of a reduced amplitude or delayed peak of the N450 (Mager, et al., 2007; West, 2004). These findings, taken together with age-related behavioural deficits in RT and accuracy, lend support for the idea that the conflict monitoring system is compromised in later adulthood. More direct support for this hypothesis comes from fMRI research showing reduced cortical volume in the ACC in older adults, and an association between ACC volume and Stroop performance (Elderkin-Thompson, Ballmaeir, Hellemann, Pham, & Kumar, 2008). What is less clear is whether the conflict-related N2 ERP component changes with age as very few studies have explored this issue. In only a few Go/Nogo studies there is some evidence of a delay in the peak of the N2 component, and/or reduction in N2 amplitude (Falkenstein, Hoormann, & Hohnsbein, 2002; Hämmerer, Li, Müller, & Lindenberger, 2010). Although to date this finding is sparse, it is consistent with the evidence that other conflict-related ERP components are diminished in later adulthood. Thus, it is reasonable to predict that aging has a significant effect on the efficiency of the N2, and that other paradigms that induce conflict will reveal similar age differences.

3.2.3 Relationship between Conflict Monitoring and Motor Performance with Age

A recent topic of interest in the cognitive neuroscience literature is the influence of cognitive control, and conflict monitoring on the overt motor responses that are inherently required in most pre-potent response tasks. The approach in this type of work is to use either electrophysiological measures of motor performance, or motion analyses to explore motor output variables during pre-potent response suppression. For example,

Szücs, Soltész, and White (2009) used concurrent electromyographic and EEG recording to explore whether conflict resolution occurs at the level of the stimulus processing or response level in a manual version of the Stroop task. The data revealed that incorrect response hand EMG activity was generated during incongruent trials and that this activity was related to task performance. That is, on incongruent trials with slower RT muscle activity was observed in both correct and incorrect response hands. This suggests that the conflicting stimulus dimensions were processed up to response preparation during which conflict resolution took place. Thus, it seems likely that a conflict detection mechanism influenced motor performance by triggering the abandonment of the incorrect response in favor of the correct response. This finding lends support for our proposal that conflict monitoring can trigger online adjustments in response preparation and execution processes.

We recently conducted a series of experiments that provide data consistent with this hypothesis. Specifically, we developed a multi-finger sequencing task and used motion capture recordings to conduct kinematic analyses of pre-potent response suppression. Briefly, participants are trained to associate a particular pair of key presses in order to generate a pre-potent motor response. Participants are then presented with key presses that violate the pre-potent pair. Motion capture recordings were used to decompose movements into response planning (latency from stimulus to movement initiation) and response execution phases (from initiation to completion of the key press). For the younger adults in those experiments conflicting responses led to longer planning times, but short execution times than the pre-potent responses (Trewartha et al., 2009; Trewartha et al., 2011). We interpreted this effect as a flexible adjustment in movement

execution parameters due to the detection of conflict. The older adults in those experiments did not shorten execution time in response to conflict. We speculated that this age difference was related to inefficient conflict monitoring mechanisms in later adulthood. The current experiment was designed to directly test this hypothesis.

3.2.4 Current Study

In the current study we explored both neurophysiological correlates of conflict processing and kinematic decomposition of motor responses by acquiring concurrent EEG and motion capture data. Synchronization of these recordings allowed us to explore the time-course of the conflict-related ERP components in relation to the trajectory of the movements themselves. In this experiment we asked younger and older adults to perform a modified version of the tasks used in our previous work (Trewartha et al., 2009; Trewartha et al., 2011). Specifically, in the Trewartha et al. (2009) study we embedded the conflicting response within random sequences, whereas we embedded the conflicting responses in pre-potent pairs in the Trewartha et al. (2011) experiment. For the current study, we explored the effect of these contextual differences by directly comparing both conditions in one experiment.

The current experiment was designed to examine the following hypotheses: 1) Interference effects during the conflicting responses will be larger when embedded in pre-potent pairs, than random sequences, and older adults will experience larger interference effects than younger adults. 2) Conflict monitoring mechanisms contribute to the pre-potent response suppression of younger and older adults during this multi-finger sequencing task. 3) Age-related reductions in conflict monitoring efficiency contribute to older adults' performance declines on the conflicting responses. 4) The context in which

participants are exposed to conflicting responses influences the involvement of conflict monitoring processes. 5) Conflict detection triggers the adjustments in movement execution observed in the younger adults.

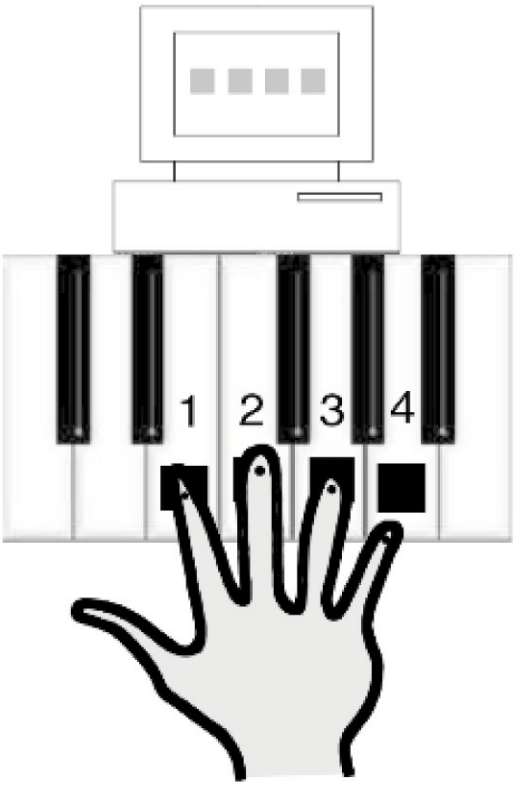
3.3 Method

3.3.1 Participants

Seventeen younger (18-32 years old, $M = 22.4$, $SD = 2.8$), and 16 older adults (66-81 years old, $M = 72.6$, $SD = 5.0$) gave informed consent to participate in this study, which was approved by Concordia University's Human Research Ethics Committee. The younger adult group consisted of 11 females, and 6 males, whereas the older adult group included 13 females and 3 males. Participants were right-handed, free from physical and neurological conditions affecting finger or hand movements, had less than three years of musical experience, and had not been practicing in the past 10 years.

3.3.2 Apparatus, Motion Capture, and Electroencephalogram (EEG) Recordings

A custom response box was built to mimic certain physical properties of the keys on a standard piano-type keyboard, including the height, length, width, resistance and spacing between keys. For the purposes of the current experiment, only 4 of the 5 keys were used (the outermost, 5th key was removed). Participants made sequences of key-presses using the four fingers of their right hand on four consecutive keys on the response box. Four dark-grey, 3" x 3" boxes oriented horizontally on a 17" flat screen monitor represented each of their fingers in a left-to-right manner. Each box, and finger, also corresponded to one of the four keys on the response box on which pieces of Velcro were affixed to act as tactile cues to aid participants in remaining on the keys (see Figure 3.1).



Examples of response pairs in each condition

Condition	Example Sequence	Response Type Breakdown
Random Baseline (15 trials)	4 2 1 3 2 1 4 1 2 3	150 random responses
Pre-potent Baseline (15 trials)	1 2 1 2 1 2 1 2 1 2	75 pre-potent responses
Pre-potent Reminder (5 blocks of 5 trials)	1 2 1 2 1 2 1 2 1 2	125 pre-potent responses
Conflict in Repeated (3 blocks of 20 trials)	1 2 1 2 **1 4** 1 2 1 2	240 pre-potent responses 60 conflicting response
Conflict in Random (3 blocks of 20 trials)	4 2 1 2 **1 3** 4 3 2 4	60 pre-potent responses 60 conflicting responses 360 random responses

Note: Pre-potent responses are underlined and conflicts are in bold. Each trial is 10 key presses long.

Figure 3.1. Illustration of the experimental set-up, with a table demonstrating the different conditions presented during the experiment. The number of each response type presented in each condition is also presented.

The boxes on the screen changed color one at a time to cue which finger/key the participant should press.

When a key was pressed down it activated a switch that sent a trigger to two data acquisition computers signaling the occurrence of a response. The response triggers were sent to the EEG acquisition computer, and to a data acquisition (DAQ) card (NI USB-6221 BNC, National Instruments Inc.). Stimulus triggers were also sent to both the EEG acquisition computer and DAQ by the stimulus presentation software (Inquisit 3.0.4.0 Millisecond Sofware LLC. Seatle, WA). During performance of the task, movement data were recorded (200 Hz) using a 3-D motion capture system (VZ3000; Phoenix Technologies Inc., Burnaby, BC, Canada) that tracked the movement of light-emitting diode (LED) markers placed on each finger nail of the right hand. In order to synchronize the motion capture data with stimuli and responses, a program was custom written in C# on version 1.1 of the Microsoft .NET Framework. This program recorded the motion capture frame number at the time that stimulus and response triggers were received by the DAQ. Stimulus and response timings were then synchronized with the motion capture data offline using a custom written function in Matlab.

The EEG acquisition software also accepted those stimulus and response triggers and implanted codes in the EEG data stream for synchronization. A continuous EEG was recorded with an active electrode EEG system, ActiveTwo (BioSemi, Amsterdam, NL), using a 64-electrode nylon cap, sampled at 500 Hz in a DC to 100 Hz bandwidth. The EEG data was recorded relative to Common Mode Sense and Driven Right Leg (CMS/DRL) electrodes placed at the back of the head, to the left and right of electrode POz, respectively. All EEG data were re-referenced offline to the linked earlobes, and

also filtered offline for frequencies between 0.1-50 Hz. Horizontal and vertical electrooculograms (HEOG and VEOG) were recorded from electrodes placed above and below the left eye, and on the outer canthi of both eyes. These HEOG and VEOG recordings were used to monitor eye movements, and trials with HEOG activity exceeding +/- 75 μV were rejected. Any excessive VEOG artefacts (i.e., eye blinks) were corrected using a spatial filter correction technique (Method 2, NeuroScan Edit 4.3 manual, 2003) in order to retain a sufficient number of trials. Trials with EEG activity and other motion artefacts exceeding +/- 100μV were rejected.

3.3.3 Procedures

Participants completed a total of thirteen blocks, without performance feedback, during which each trial consisted of a 10-key press sequence. They were instructed simply to follow along as each box lit up and press all the way down on the corresponding key, with the corresponding finger as quickly and accurately as possible. Stimulus duration was 400 ms, with a 400 ms inter-stimulus interval (ISI), and a 3000 ms pause between each trial. The experiment consisted of 5 different conditions: a) Random baseline; b) Pre-potent baseline; c) Pre-potent response reminder; d) Conflict in Repeated; and e) Conflict in Random. For each participant the first block was the Random block that consisted of 15 random trials to act as a baseline of the ability to follow along with the stimuli in a completely unpredictable fashion. The second block was a "pre-potent response acquisition" block during which a single pair of key presses was presented repeatedly, five times in each trial, for 15 trials. This block induced a pre-potent pair of key presses that could be used to create conflicting responses for subsequent blocks.

The remaining 11 blocks alternated between conflicting blocks and short pre-potent response reminder blocks. In the reminder blocks the pre-potent pair was presented five times in each trial in the same manner as the pre-potent acquisition block but was only 5 trials long. The conflict blocks consisted of 20 trials each in two conditions: 1) in the "Conflict-in-Repeated" condition, a single conflicting pair was embedded within repeated pre-potent pairs in each 10 key press trial; 2) in the "Conflict-in-Random" blocks the conflicting pair and one pre-potent response pair were embedded within random key presses. These conditions allowed us to investigate the effect of the context in which participants were exposed to the conflicting responses. Conflicting responses were defined as the same first key press from the pre-potent pair, followed unexpectedly by an alternate key press. The serial position of the conflict within each trial was determined randomly, and an equal number of conflicting responses were presented using either of the two alternate fingers. After completing the Random and pre-potent baseline blocks, each participant performed a series of alternating Conflict-in-Random and Conflict-in-Repeated blocks, each time with an intervening pre-potent reminder block. The block order was counterbalanced across participants such that they started either with a Conflict in Random, or Conflict-in-Repeated block.

3.3.4 Data Analyses: Motion Capture

The data were separated into a total of eight different response types: 1) Random Baseline; 2) Pre-potent Baseline; 3) Pre-potent Reminder; 4) Pre-potent-in-Repeated; 5) Pre-potent-in-Random; 6) Random-in-Random; 7) Conflict-in-Repeated; and 8) Conflict-in-Random. All responses were defined as the second press in each pair except for the

random responses for which all responses were included. The total numbers of each response type are presented in Figure 3.1.

The motion capture frames were used to synchronize the stimulus and response triggers with the movement data. The kinematic analysis tools were custom written in Matlab, and adapted in part from the tools developed for our previous experiments (Trewartha et al., 2009; Trewartha et al., 2011). The current data were first processed into 900 ms epochs around each stimulus from 100 ms before the stimulus to 800ms after the stimulus. The specific response finger was then identified as the LED marker with the maximum peak at the time of the response trigger. In the event that a response trigger was missing from an epoch a peak detection algorithm (as described in Trewartha et al., 2009) was employed to determine if there was a key press that failed to activate the switch (i.e., wasn't pressed fully). Briefly, key-presses were identified as local minima (i.e., troughs) among samples that were more than three standard deviations below the baseline in the vertical (z) dimension. In the event that more than one response occurred in an epoch, the first key-press after the stimulus was accepted as the response. A response was considered accurate if the correct finger made a response while the stimulus was on the screen or during the ISI. Planning and execution time were calculated using the time of the full key press (i.e., trough) and the movement initiation time. Movement initiation was defined by a backward search from the trough to the point at which the movement was below 5% maximum velocity of the key press. Planning time was then defined as the elapsed time from the stimulus to movement initiation, and execution time defined from movement initiation to full response. These time-course variables are only presented for correct responses.

3.3.5 Data Analyses: ERP

ERP analyses were conducted using Scan (software by Compumedics Neuroscan, Charlotte, NC, USA). Akin to the movement data, stimulus-locked EEG epochs of 900 ms (-100 ms to 800 ms) were obtained to assess waveforms difference between various stimulus/response types. Average waveforms were computed only for trials in which there was a correct response for each participant. Averages were baseline corrected to a 0 μV average of the 100 ms pre-stimulus interval. In order to explore age differences in stimulus-related conflict detection processes, the mean average amplitude was computed in the interval from 150-300 ms after the stimulus onset (i.e., one of the boxes lighting up) in order to characterize the N2 component. Consistent with the N2 literature reviewed above (see Folstein & van Petten, 2008), the average amplitude in this interval was compared between correct and incorrect trials over the anterior, midline electrode sites: Fz and FCz. In order to allow for possible age differences in the distribution of the N2 we also made comparisons at more posterior midline sites Cz, and CPz. The peak amplitude within this interval was also recorded in order to compare differences in the peak and, importantly, the latency of the N2 component between the age groups.

3.4 Results

The results are organized into three sections. First, the motion capture data were analyzed to explore the movement patterns of younger and older adults. Second, the ERP data provide an assessment of the role of conflict monitoring mechanisms during pre-potent response suppression in conflict trials. Third, the motion capture and ERP data are combined to explore the relationship between conflict monitoring and movement patterns in younger and older adults. The ANOVA designs for each section are described

separately, and for each test of simple main effects, comparisons are reported with a Bonferroni correction.

3.4.1 Motion Capture Data

The first set of behavioral analyses provides a comparison of younger and older adults' ability to perform in the baseline random, and pre-potent response conditions. The second set of behavioral analyses presents a direct exploration of the effect of the context in which participants encountered conflicting responses by comparing younger and older adults' performance during the Conflict-in-Repeated, and Conflict-in-Random conditions. For each set of analyses we conducted separate ANOVAs on each behavioural performance measure: accuracy, planning time, and execution time.

Baseline comparisons. To explore the baseline ability of younger and older adults' performance of random sequences (the least predictable), and repeated pre-potent responses (the most predictable) we conducted an age group x responses type (random versus pre-potent) ANOVA for each dependent variable (see Table 3.1 for means and standard deviations). For accuracy there was an overall main effect of response type, $F(1,30) = 7.78$, $p < .01$, $\eta_p^2 = 0.21$, such that both age groups were more accurate on the pre-potent than random responses, but no other comparisons were significant (all ps > 0.14). In terms of planning time there were significant main effects of age group, $F(1,30) = 11.38$, $p < .01$, $\eta_p^2 = 0.28$, and response type, $F(1,30) = 200.86$, $p < .001$, $\eta_p^2 = 0.87$, and a significant interaction between age group and response type, $F(1,30) = 6.86$, $p < .05$, $\eta_p^2 = 0.19$. Post-hoc comparisons revealed that older adults spent more time planning the random responses, $t(30) = -4.37$, $p < 0.001$, but not the pre-potent responses ($p > 0.12$). For execution time there was a significant interaction between age group and

Table 3.1

Means and standard deviations for the behavioral measures in non-experimental response types.

Response Type	Age Group	Accuracy (%)		Planning Time (ms)		Execution Time (ms)	
		M	*SD*	*M*	*SD*	*M*	*SD*
Random Baseline	Younger	87.5	19.8	257.0	34.8	212.6	46.9
	Older	86.4	19.1	360.2	42.0	206.1	47.4
Pre-potent Baseline	Younger	94.5	10.0	141.4	36.4	246.9	49.2
	Older	97.6	3.8	174.7	72.5	197.7	65.0
Pre-potent Reminder	Younger	93.3	11.7	128.0	33.2	212.3	37.6
	Older	97.5	3.9	175.7	45.6	163.1	38.0
Random in Random	Younger	93.8	7.1	249.7	33.0	201.5	35.4
	Older	92.8	5.7	359.4	44.6	193.9	40.5

Note: Means and standard deviations for each age group are presented for the Baseline Random responses (Random Baseline), baseline pre-potent responses (Pre-potent Baseline), the pre-potent responses presented in the reminder blocks (Pre-potent Reminder), and the random responses in the Conflict-in-Random experimental condition (Random in Random). Although the pre-potent reminder, and Random in Random responses were not entered into any statistical comparisons, they are presented here for completeness.

response type, $F(1,30) = 7.25$, $p < .05$, $\eta_p^2 = 0.20$, such that younger adults spent more time executing the pre-potent responses than older adults, but the age groups were equivalent on the random responses ($p > 0.13$). These findings show that older adults need more time to plan movements to completely unpredictable responses than younger adults, but importantly, the age groups did not differ in their accuracy or planning time to produce the pre-potent baseline responses. In addition, as we observed in our previous work (Trewartha, et al., 2009; Trewartha et al., 2011) younger adults spent more time executing the pre-potent responses than older adults.

Context Effects. The novel behavioral analysis for the current study is to determine the effect of the context in which conflicting responses are encountered on younger and older adults' pre-potent response suppression. To explore this issue we compared the conflicting and pre-potent responses across age and experimental conditions (Figure 3.2). That is, we conducted an age group (younger versus older adults) x context (Conflict-in-Repeated versus Conflict-in-Random) x response type (conflicting versus pre-potent) ANOVA for each behavioural measure.

In terms of accuracy, there was a main effect of response type such that participants were more accurate during the pre-potent responses compared to conflicting responses, $F(1,30) = 8.62$, $p < .01$, $\eta_p^2 = 0.22$, and a main effect of age group such that younger adults were more accurate than older adults, $F(1,30) = 10.1$, $p < .01$, $\eta_p^2 = 0.25$. In addition, there was a significant interaction between age and response type, $F(1,30) = 5.2$, $p < .05$, $\eta_p^2 = 0.15$, and a significant three-way interaction between age, context, and response type, $F(1,30) = 6.0$, $p < .05$, $\eta_p^2 = 0.17$. Post-hoc comparisons revealed that the

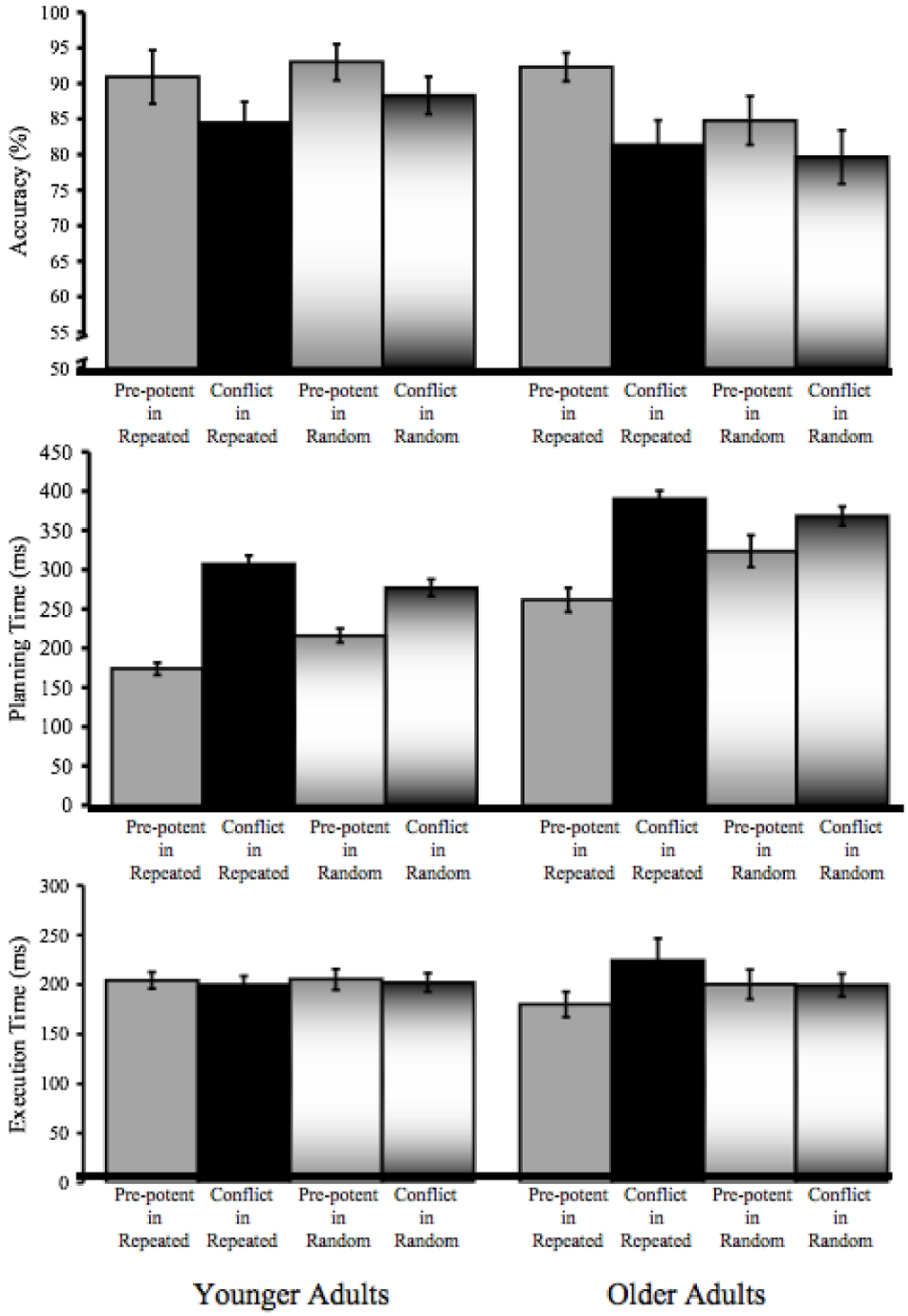


Figure 3.2. Figure showing the averages for each age group, and each behavioural measure for the conflicting and pre-potent responses in the Conflict-in-Repeated, and Conflict-in-Random conditions. Error bars represent standard error of the mean.

younger adults' accuracy did not differ between pre-potent and conflicting responses, either in the Conflict-in-Repeated, or Conflict-in-Random condition ($p > 0.27$). The older adults were less accurate on the conflicting than pre-potent responses in the Conflict-in-Repeated condition, $t(14) = -4.04$, $p < 0.001$. This pattern was also marginally significant for older adults in the Conflict-in-Random condition, $t(14) = -1.96$, $p = 0.057$. These results reveal that in terms of response accuracy, the younger adults did not show a conflict effect in either condition. More importantly, for the older adults the conflicting responses were most interfering when they were embedded in pre-potent pairs of key presses compared to random sequences.

A main effect of response type revealed that planning time was longer for conflicting responses than pre-potent responses overall, $F(1,30) = 136.28$, $p < .001$, $\eta_p^2 = 0.82$. The main effect of context revealed that planning time was longer during the Conflict-in-Repeated compared to Conflict-in-Random condition, collapsed across response type, $F(1,30) = 12.4$, $p < .01$, $\eta_p^2 = 0.29$. Older adults also exhibited longer planning time than younger adults, as evidenced by a main effect of age group, $F(1,30) = 27.85$, $p < .001$, $\eta_p^2 = 0.48$. There was also a significant interaction between age group and context, $F(1,30) = 4.46$, $p < .05$, $\eta_p^2 = 0.13$, such that younger adults did not differ between the two conditions ($M_{diff} = 6$ ms, $p > 0.31$), whereas older adults had longer planning time overall during the Conflict-in-Random condition compared to Conflict-in-Repeated condition, $M_{diff} = 24$ ms, $t(14) = -3.87$, $p < 0.001$. Finally, there was a significant interaction between response type and context, $F(1,30) = 50.64$, $p < .001$, $\eta_p^2 = 0.63$, such that the interference effect was largest in the Conflict-in-Repeated condition, $M_{diff} = 143$ ms, $t(30) = -14.85$, $p < 0.001$, compared to Conflict-in-Random condition,

M_{diff} = 57 ms, $t(30) = -5.18$, $p < 0.001$, collapsed across age group. In terms of context effects, these comparisons reveal that the conflicting responses were most interfering for both age groups when they were embedded in pre-potent pairs of key presses, than random sequences.

For execution time, the only significant effects were observed for the interaction between response type and context, $F(1,30) = 5.46$, $p < .05$, $\eta_p^2 = 0.15$, and a three-way interaction between age, context, and response type, $F(1,30) = 6.17$, $p < .05$, $\eta_p^2 = 0.17$. Post-hoc comparisons revealed that the only significant difference was longer execution time for older adults for the conflicting responses in the Conflict-in-Repeated, compared to Conflict-in-Random condition, M_{diff} = 23 ms, $t(14) = 2.17$, $p < 0.05$. No other comparisons were significant ($p > 0.08$).

To summarize the behavioural findings, the current data replicate our previous observations (Trewartha et al., 2009; Trewartha et al., 2011) that older adults have more difficulty than younger adults suppressing a pre-potent key press in order to perform a conflicting key press. Those findings are extended by the current experiment to show that the context in which those conflicts occur has a greater effect on older adults' pre-potent response suppression than younger adults in terms of response accuracy, and movement execution time. With this in mind, we turn to the ERP data in order to explore whether or not this pre-potent response suppression deficit in aging is related to conflict monitoring.

3.4.2 ERP Data

Given that there were age-related differences in the movement patterns exhibited during conflicting responses, we examined the ERP data to determine if these behavioural differences were related to the strength of the conflict-related N2 component.

More specifically, we explored age differences in stimulus-locked ERP waveforms following the conflicting stimuli and compared them to the waveforms generated by other types of stimuli in each conflict condition. As can be observed in Figure 3.3, there was a negative deflection in the averaged waveform, peaking between 200-300 ms after the conflicting stimuli for both younger and older adults over midline sites Fz, FCz, Cz, and CPz in the Conflict-in-Repeated condition. It is important to note that this negative deflection appears to occur for the Conflict-in-Repeated stimuli, but not for the pre-potent stimuli in that condition. Based on the polarity, timing, and topographical distribution, this component is taken to be the N2. This provides evidence that a conflict monitoring mechanism is involved in processing the conflict during the Conflict-in-Repeated condition. However, another important observation is that the overall morphology of the waveform differs between the age groups. Younger adults exhibit an N2 component of similar amplitude over all four midline electrode sites, whereas the amplitude of the N2 in the older adults appears to be maximal at more posterior sites, and is almost absent at the most anterior site (Fz). In addition, older adults, but not younger adults, exhibit a large P3 component immediately following the N2 waveform, between 300-500 ms post-stimulus, that is also largest at the posterior sites. Both of these components are compared between the age groups in the statistical analyses presented below. Another observation from visual inspection of the figures is that the waveform appears quite different for each age group during the Conflict-in-Random condition (Figure 3.4) compared to the Conflict-in-Repeated condition (Figure 3.3). The N2 appears to be absent in the younger adults in the Conflict-in-Random condition, but an N2-like waveform is evident for older

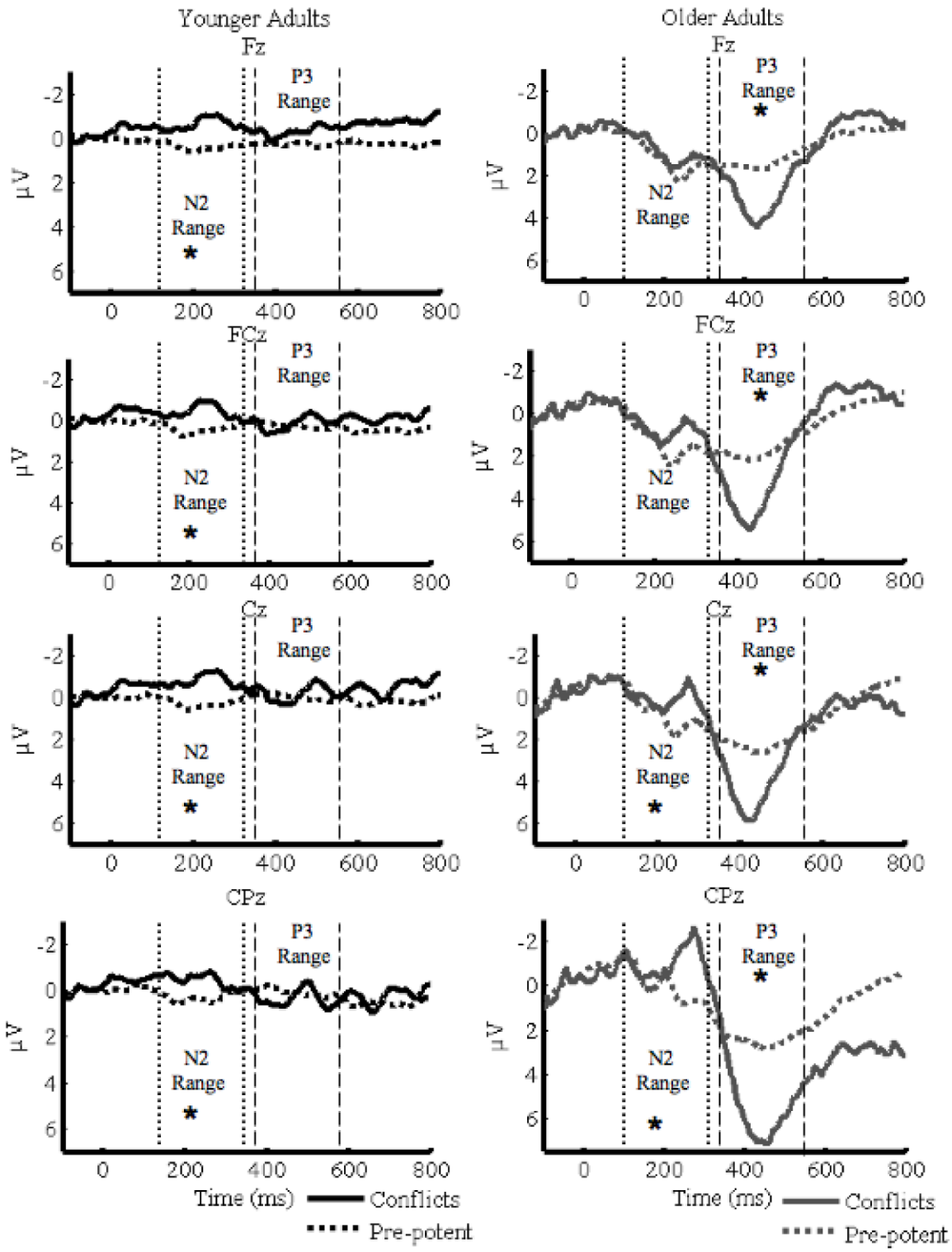


Figure 3.3. Stimulus-locked, grand averaged waveforms for younger and older adults comparing the pre-potent and conflicting responses in the Conflict-in-Repeated condition. The N2, and P3 component intervals are marked, and significant components are demarcated with an asterisk at the $p < 0.05$ level.

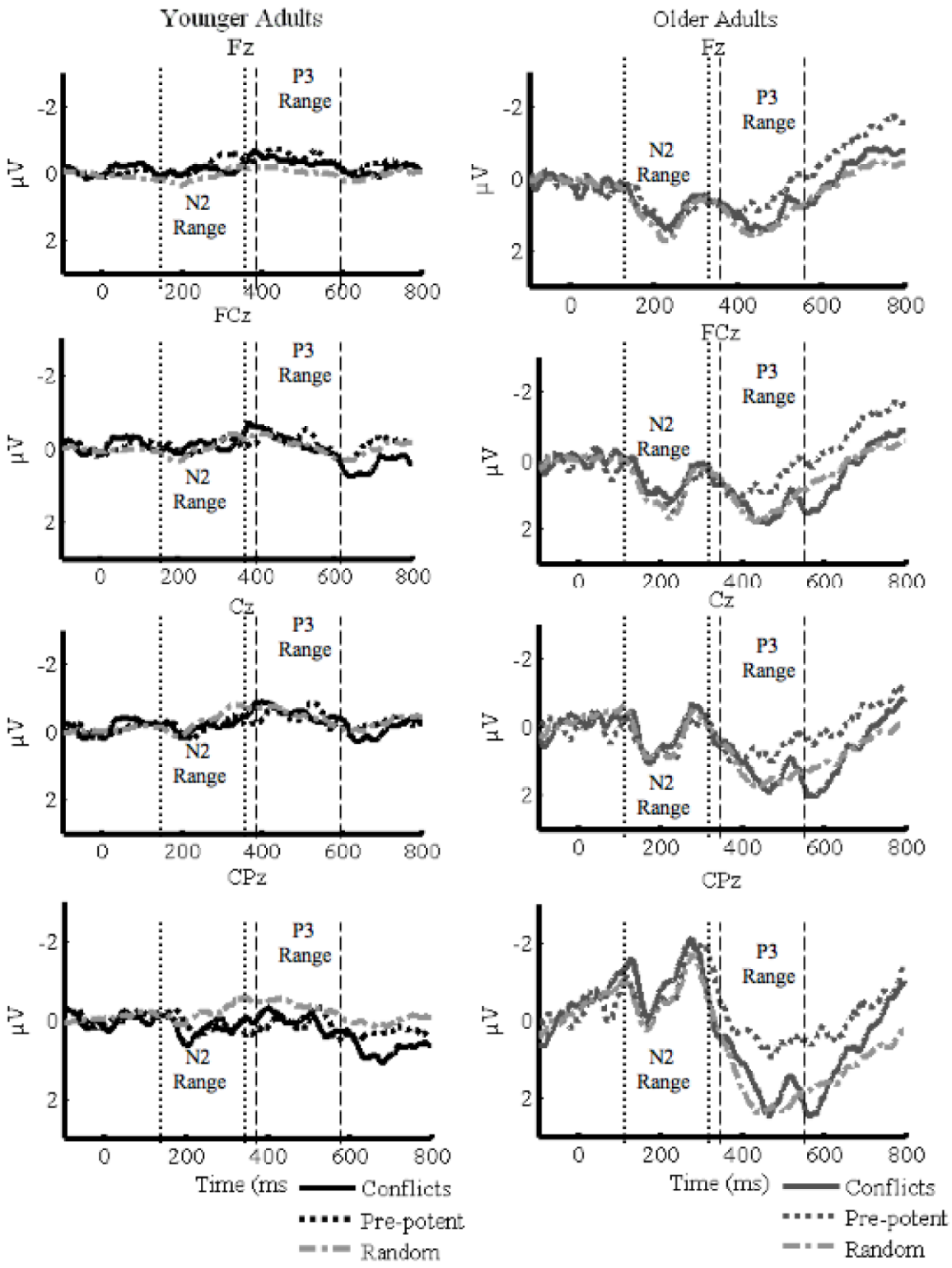


Figure 3.4. Stimulus-locked, grand averaged waveforms for younger and older adults comparing the pre-potent and conflicting responses in the Conflict-in-Random condition. The N2, and P3 component intervals are highlighted.

adults at all four midline sites, for the random, pre-potent, and conflicting responses. This observation is important as it suggests that different cognitive processes are involved when the conflicting responses are embedded within random sequences, compared to pre-potent responses. The following two sub-sections present statistical comparisons to verify this visual inspection of the waveforms.

Conflict Embedded in Repeated Pairs. Since the largest behavioral interference effects occurred for the Conflict-in-Repeated condition, we first explored whether those conflicting stimuli generated a robust N2 component. This first set of ERP analyses test the predictions that conflict monitoring contributes to pre-potent response suppression; and that age differences in conflict monitoring efficiency can explain age-related declines in conflicting response performance. To this end we compared the stimulus-locked waveform following conflicting stimuli to pre-potent stimuli in the Conflict-in-Repeated condition between the age groups. More specifically, we conducted an age group (younger versus older) x response type (conflict versus pre-potent response) x electrode site (Fz, FCz, Cz, and CPz) ANOVA on the average amplitude of the waveform in the 150-300 ms post-stimulus interval. This omnibus ANOVA revealed a main effect of response type such that the amplitude was more negative for the conflicting compared to repeated responses, $F(1,29) = 6.23$, $p < .05$, $\eta_p^2 = 0.18$, and a main effect of electrode site, $F(3,27) = 5.58$, $p < .01$, $\eta_p^2 = 0.39$. There was also a significant interaction between age group and electrode site, $F(3,27) = 6.00$, $p < .01$, $\eta_p^2 = 0.41$. From visual inspection of Figure 3.3 it is clear that there are striking differences in topography between the age groups. In fact, there was a marginally significant three-way interaction between age group, response type, and electrode site, $F(1,29) = 1.97$, $p = .08$, $\eta_p^2 = 0.19$. In light of

these obvious differences, we chose to compare the averaged waveforms of the age groups at each electrode site. That is, we conducted an age group (younger versus older) x response type (conflict versus pre-potent response) ANOVA on the average amplitude of the waveform in the 150-300 ms post-stimulus interval for each midline electrode site. These statistical comparisons revealed that at Fz there was a significant effect of response type, $F(1,29) = 7.43$, $p < .05$, $\eta_p^2 = 0.20$, age group, $F(1,29) = 13.78$, $p < .01$, $\eta_p^2 = 0.32$, and a significant interaction between response type and age, $F(1,29) = 10.55$, $p < .01$, $\eta_p^2 = 0.27$. Bonferroni corrected post-hoc comparisons revealed that younger adults had a significantly more negative amplitude for the conflicting responses compared to the pre-potent responses, $t(16) = 4.44$, $p < 0.001$, but older adults did not differ between the response types ($p > 0.72$). This finding reveals that at the most anterior midline site (Fz), younger adults exhibit a larger N2 than older adults to the conflicting responses embedded in pre-potent pairs of key presses. The same pattern of effects was observed at FCz with a marginally significant effect of response type, $F(1,29) = 3.73$, $p = .06$, $\eta_p^2 = 0.11$, a significant effect of age group, $F(1,29) = 5.30$, $p < .05$, $\eta_p^2 = 0.16$, and a marginally significant interaction between response type and age, $F(1,29) = 4.00$, $p = .055$, $\eta_p^2 = 0.12$. Again, post-hoc comparisons revealed that there was a larger negative amplitude for conflicting compared to pre-potent response for younger adults, $t(16) = 2.92$, $p < 0.01$, but not older adults ($p > 0.96$). For the other two electrode sites there was only a significant effect of response types (Cz: $F(1,29) = 5.44$, $p < .05$, $\eta_p^2 = 0.16$; CPz: $F(1,29) = 5.41$, $p < .05$, $\eta_p^2 = 0.16$). Thus, at posterior midline sites both age groups had a significantly larger N2 on conflicting compared to pre-potent responses. No other comparisons were significant for these two electrode sites (all $p > 0.15$).

It is clear from these results that the amplitude of the N2 is diminished in older adults, especially over more anterior midline sites compared to younger adults. From visual inspection of Figure 3.3 it also appears that there may be a latency shift of the N2 with aging. Figure 3.5 shows an overlay of the younger and older adults' grand averaged waveforms at Cz, with the average movement time-course also included for demonstration purposes. To explore this possible latency shift we determined the latency of the peak of the N2 for conflicting responses, defined as the time of the minimum amplitude between 150-300 ms post-stimulus, and compared this latency between the age groups using t-tests for each midline electrode. The results revealed a significantly longer N2 latency for older compared to younger adults at Fz, $t(30) = 3.39$, $p < 0.01$, FCz, $t(30) = 2.27$, $p < 0.05$, marginally at Cz, $t(30) = 2.27$, $p = 0.067$, and a longer latency at CPz that failed to reach significance ($p > 0.28$).

The second interesting, albeit unexpected observation from Figure 3.3 is that older adults exhibited a large P3 following the N2 on conflicting responses that is not clearly present in the younger adults. As the P3 is often associated with attentional processes it is possible that older adults' attention was captured to a greater extent by the conflict than younger adults. To explore this component further we calculated the average amplitude of the averaged waveform from 300-500 ms post-stimulus and compared younger and older adults between conflicting and pre-potent responses in the Conflict-in-Repeated block with a 2 (age group) x 2 (response type) ANOVA. The analysis

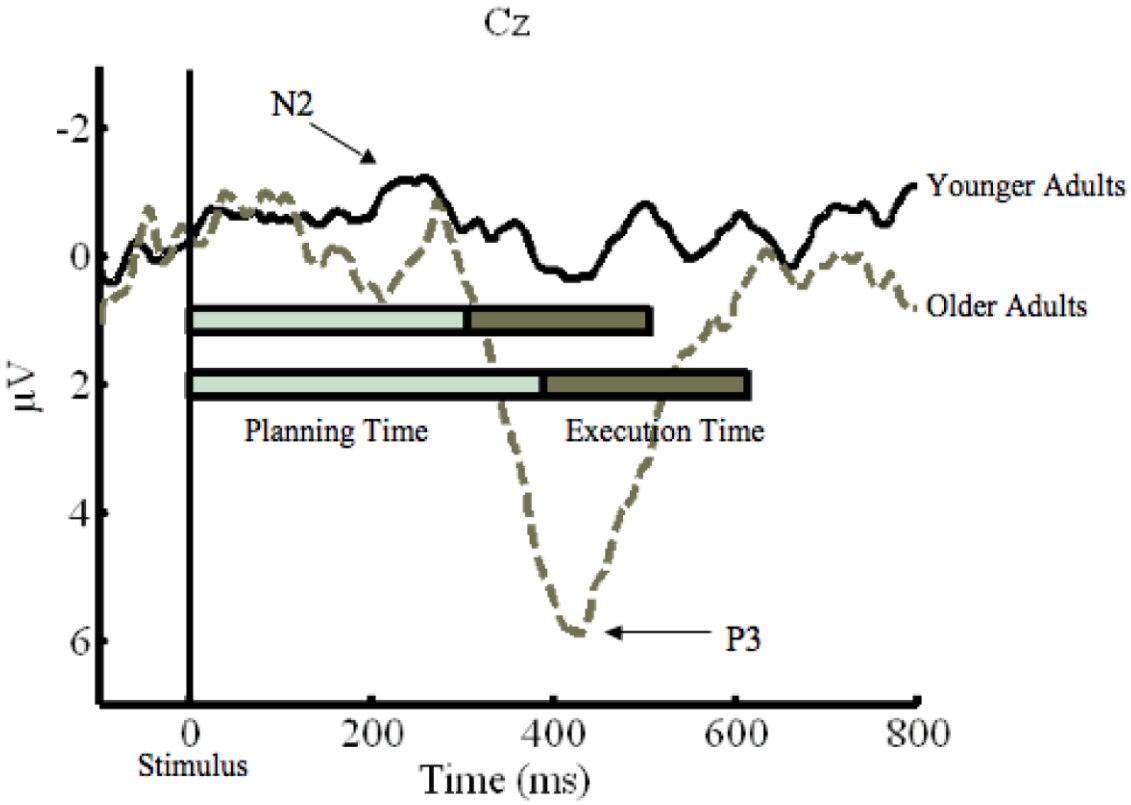


Figure 3.5. Presents the stimulus-locked, grand averaged waveform for younger and older adults for the Conflict-in-Repeated responses at electrode site Cz. This figure demonstrates the increased latency in the N2 component for older, compared to younger adults. Behavioral data are also superimposed on the ERP waveforms to demonstrate the averaged planning (light grey bars) and execution time (dark grey bars) for each age group (top bars are the younger adults, and the bottom bars are the older adults) on these responses. This demonstrates the time-course of the neural and behavioral responses to the stimuli. The point at which the light and dark grey bars join represents the initiation of the movement, and the end of the dark grey bar, on the right, represents the overall reaction time.

confirmed that older adults had a significantly larger P3 than younger adults (Fz: $F(1,29) = 11.02$, $p < .01$, $\eta_p^2 = 0.28$; FCz: $F(1,29) = 6.59$, $p < .05$, $\eta_p^2 = 0.19$; Cz: $F(1,29) = 11.17$, $p < .01$, $\eta_p^2 = 0.28$; and CPz: $F(1,29) = 14.43$, $p < .01$, $\eta_p^2 = 0.34$). At Cz and CPz there was a significant main effect of response type, $F(1,29) = 11.70$, $p < .01$, $\eta_p^2 = 0.28$, and $F(1,29) = 14.43$, $p < .01$, $\eta_p^2 = 0.34$, respectively. There was also a significant interaction between response type and age (Fz: $F(1,29) = 9.40$, $p < .01$, $\eta_p^2 = 0.25$; FCz: $F(1,29) = 4.37$, $p < .05$, $\eta_p^2 = 0.13$; Cz: $F(1,29) = 7.28$, $p < .05$, $\eta_p^2 = 0.20$; and CPz: $F(1,29) = 14.32$, $p < .01$, $\eta_p^2 = 0.34$). The post-hoc comparisons revealed that this interaction was driven by a significant difference between conflicting and pre-potent responses for older adults (Fz: $t(14) = 2.90$, $p < 0.01$; FCz: $t(14) = 2.57$, $p < 0.05$; Cz: $t(14) = 3.23$, $p < 0.01$; CPz: $t(14) = 5.32$, $p < 0.001$) but not younger adults (all $p > 0.18$). These comparisons reveal that there was a significant conflict-related P3 for older adults, but not younger adults.

To summarize the ERP data thus far, when conflicting responses were embedded in pre-potent pairs of key presses, younger and older adults exhibited an N2 peak between 200 and 300 ms after stimulus presentation. This N2 was smaller in amplitude and delayed in the older participants relative to younger adults, especially over fronto-central regions. There was also a significant P3 component between 300-600 ms post-stimulus for older, but not younger adults. Therefore, the N2 data provide evidence that a conflict monitoring mechanism contributes to the detection of conflict following stimulus presentation in the younger adults. However, in the older adults increased interference on conflicts embedded in pre-potent pairs may be in part due to diminished conflict monitoring mechanism.

Conflict Embedded in Random Sequences. One of the goals of the current study was to explore the effect of the context in which conflicting responses are encountered on younger and older adults' performance. Behaviorally, the results revealed that the interference effects were larger in the Conflict-in-Repeated, compared to Conflict-in-Random conditions for both groups. An additional question of interest is whether conflict monitoring played a role in the performance of the Conflict-in-Random responses as it did in the Conflict-in-Repeated responses. In order to explore this question we compared the stimulus-locked ERPs for the conflicting and pre-potent responses embedded in random sequences to the random responses themselves in a 2 (age group) x 3 (response type) ANOVA. As can be observed in Figure 3.4, the N2 that was observed for the Conflict-in-Repeated responses appears much less pronounced for the Conflict-in-Random responses, especially for younger adults. The ANOVAs revealed that the only significant effect was an overall age effect at Fz, $F(1,29) = 5.51$, $p < .05$, $\eta_p^2 = 0.16$, such that younger adults had a significantly more negative average amplitude than older adults. No other comparisons were significant (all $p > 0.14$). These data show that when the conflicting responses were embedded within random sequences neither age group exhibited a significant conflict-related N2. Although visually it appears that the older adults have an N2 waveform for conflicting responses, they also exhibited the same N2 for the pre-potent and random responses.

Direct comparison of the conflicting responses in the Conflict-in-Random and Conflict-in-Repeated blocks (Figure 3.6) revealed that at Fz there was a significant effect of age group such that younger adults had a significantly more negative average amplitude overall compared to older adults, $F(1,29) = 15.55$, $p < .001$, $\eta_p^2 = 0.35$. The

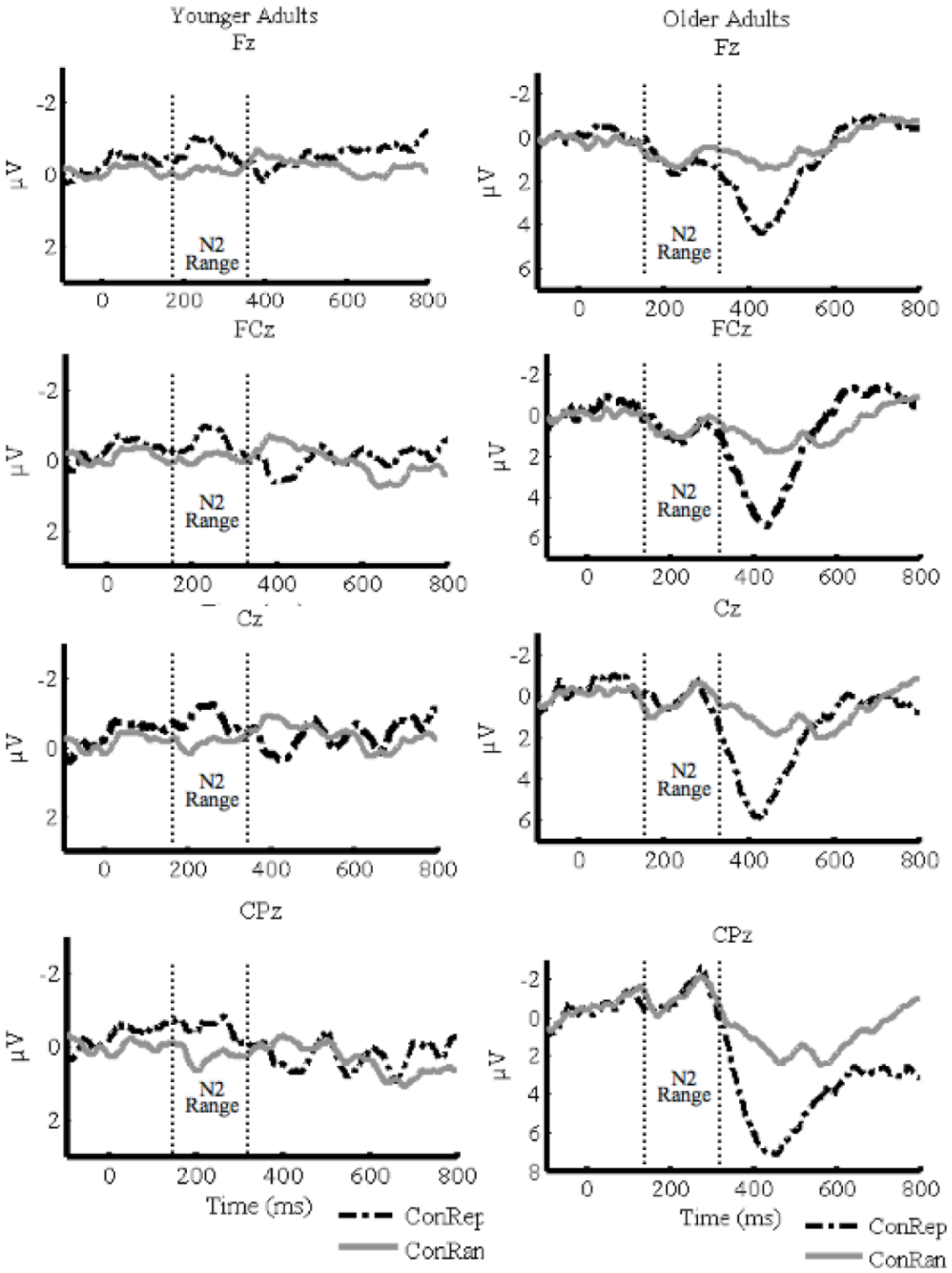


Figure 3.6. Stimulus-locked, grand averaged waveforms for younger and older adults comparing the conflicting responses in the Conflict-in-Repeated condition (ConRep) to the Conflict-in-Random condition (CanRan). The N2 component interval is highlighted.

same age effect occurred at FCz, $F(1,29) = 4.64$, $p < .05$, $\eta_p^2 = 0.14$. Importantly, there was a marginally significant interaction between age group and response type at Fz, $F(1,29) = 5.61$, $p = .056$, $\eta_p^2 = 0.12$. Post-hoc comparisons revealed that the age difference was greater for the Conflict-in-Repeated responses, $t(30) = 4.19$, $p < 0.001$, than the Conflict-in-Random responses, $t(30) = 2.29$, $p < 0.05$. No other comparisons were significant (all $p > 0.08$). These results confirm the above findings that older adults exhibited a diminished N2 at the fronto-central electrode site Fz for the conflicting responses embedded in repeated pairs of key presses.

Overall, these ERP data suggest that the conflicting responses in the current paradigm only lead to a significant conflict-related N2 component when they were embedded in repeated pairs of key presses, and this N2 was diminished in the elderly over fronto-central sites. The stimulus-locked waveforms for the conflicts embedded in random sequences did not differ from the pre-potent or random responses for either age group. This suggests that at the neuronal level, the conflicts and pre-potent responses in this context were treated in the same way as random responses. Further confirmation of this interpretation comes from a direct comparison of the average amplitude between 150-300 ms post-stimulus for the Conflict-in-Random responses to the random baseline responses in a 2 (age group) x 2 (response type) ANOVA. The only significant difference was a more positive average amplitude for the older compared to younger adults overall at Fz, $F(1,29) = 8.70$, $p < .01$, $\eta_p^2 = 0.23$. No other differences were significant (all $p > 0.09$).

Combined motion capture and ERP data. One of the most novel features of the current study is the concurrent acquisition of motion capture and ERP data. This

combination allowed us to directly assess the relationship between movement patterns of younger and older adults, and conflict monitoring mechanisms. As noted above, during the Conflict-in-Repeated condition we observed a robust conflict-related N2 component in the younger adults at all four midline sites. In the elderly participants, the amplitude of this N2 component was diminished at more anterior midline sites, and instead, had a more posterior maximal distribution. The peak of the N2 was also delayed in the older, relative to younger adults. Consistent with our hypothesis, these data indicate that the integrity of the conflict monitoring mechanism is compromised in later adulthood. However, the movement data suggested that younger adults minimize overall reaction time on conflicting responses by executing those movements more quickly than older adults.

An important, and novel question is whether conflict monitoring can trigger adjustments in movement control during conflict trials. To provide insight into this question we explored the correlation between conflict monitoring as reflected in the ERP data, and movement execution, as reflected in the motion capture data. Specifically, we calculated the Pearson correlation between the magnitude of the N2 and execution time for Conflict-in-Repeated responses. The magnitude of the N2 was quantified as the difference between the minimum peak amplitude (i.e., the most negative peak) in the 150-300 ms post-stimulus range for the conflicting and pre-potent responses. The more negative this value, the greater the difference between the response types. This correlation was calculated separately for each age group to explore age differences in the influence of conflict monitoring on movement control. We found that younger adults exhibited a significant correlation between N2 magnitude and conflicting response

execution time, $r = 0.51$, $p < 0.05$, at electrode site Fz, such that more negative (i.e., larger) N2 waveforms were related to faster execution time. However, this correlation was not significant for older adults, $r = 0.05$, $p > 0.85$ (see Figure 3.7). The same pattern of correlations was observed at FCz (younger adults: $r = 0.11$; older adults: $r = -0.04$), Cz (younger adults: $r = 0.29$; older adults: $r = -0.19$), and CPz (younger adults: $r = 0.20$; older adults: $r = -0.20$), but none of these correlations reached significance ($p > 0.25$). These correlations demonstrate that the magnitude of the N2 is correlated with the execution speed of the Conflict-in-Repeated responses at fronto-central site Fz, but only for the younger adults. This effect is evidence that conflict detection can trigger adjustments in movement control within conflict trials. It also demonstrates that the reduced amplitude of the N2 in older adults is related to the age-related decline in flexible response adaptation.

Although the older adult group as a whole didn't exhibit a correlation between N2 magnitude and execution time, it is clear that they exhibited an N2-like waveform. This observation begs the question of whether there are individual differences in the age-related declines in N2 integrity in the older adults. To explore this issue we used the motion capture data to create within-age-group median splits based on the extent to which participants were able to shorten execution time on the conflicting, compared to pre-potent responses in the Conflict-in-Repeated condition. To conduct this median split we first calculated difference scores for the execution time on the conflicting and pre-potent responses for each participant. The median value of these difference scores for each group was used to generate sub-groups that were either high or low on the ability to shorten execution time during the conflict trials. The resulting groups included 9 younger

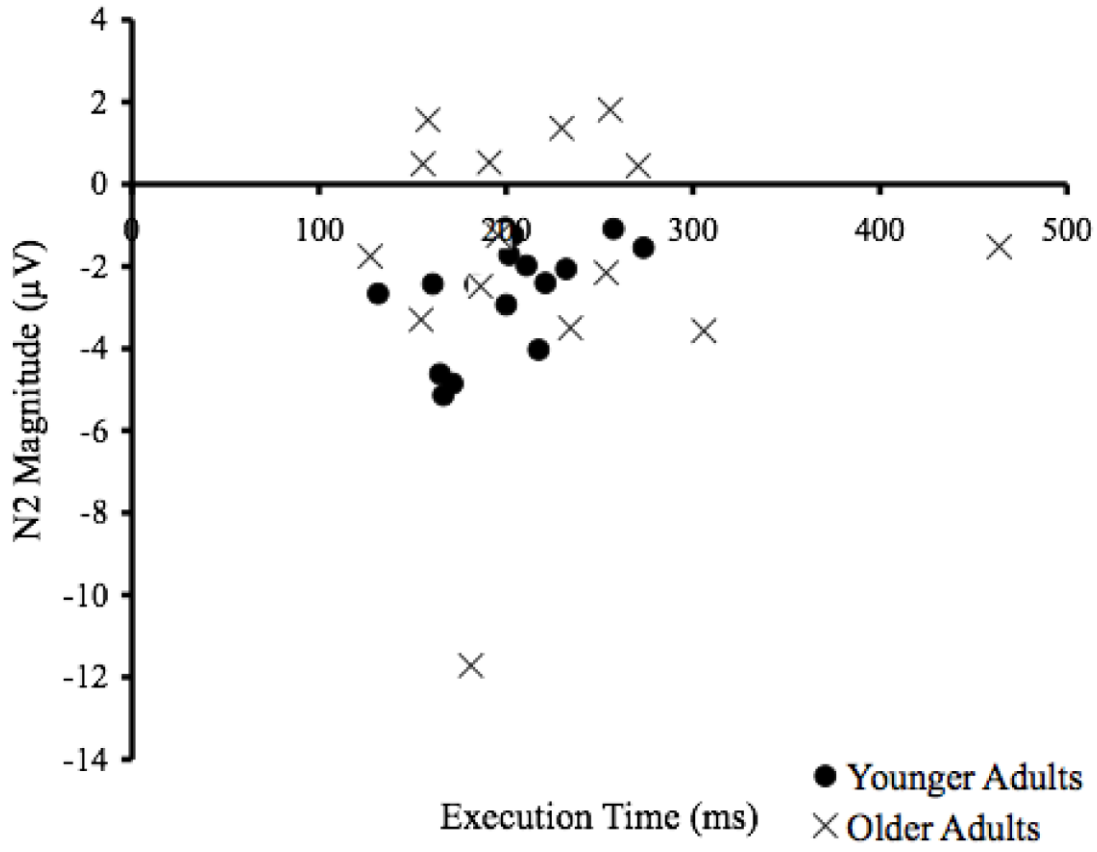


Figure 3.7. Scatter plot showing the correlation between the N2 magnitude and execution time for younger (filled circles) and older adults (x's). The N2 magnitude is quantified as the amplitude difference between the most negative peak from 150-300 ms after the conflicting and pre-potent stimuli in the Conflict-in-Repeated Condition. Execution time represents the conflicting responses in this condition.

adults who were low adapters (6 females; $M = 23.2$, $SD = 3.8$ years old), 8 younger adults who were high adapters (5 females; $M = 21.5$, $SD = 2.1$ years old), 7 older adults who were low adapters (5 females; $M = 75.2$, $SD = 4.1$ years old), and 8 older adults who were high adapters (7 females; $M = 69.9$, $SD = 4.6$ years old). We used t-tests to compare the average chronological age of the sub-groups of younger and older adults. These comparisons revealed that the low and high adapting younger adults did not differ in chronological age ($p > 0.25$), whereas the low adapting older adults were significantly older than the high adapting older adults, $t(13) = 2.19$, $p = 0.05$.

The goal of this median split analysis is to determine if a subset of the older participants who did modulate execution time exhibited a larger N2 component that is more comparable to the younger adults, than those older participants who did not adapt execution speed. To this end, we re-ran the age group (younger versus older) x response type (conflict versus pre-potent response) ANOVA on the average amplitude of the waveform in the 150-300 ms post-stimulus interval for each midline electrode site separately for individuals who were above and below the median execution time adaptability (see Figure 3.8). For the individuals who were less able to adapt execution time this analysis revealed a similar pattern as the overall ANOVA reported above. Specifically, there was a significant effect of age group at Fz, $F(1,15) = 24.16$, $p < .001$, $\eta_p^2 = 0.62$, FCz, $F(1,15) = 20.96$, $p < .001$, $\eta_p^2 = 0.58$, Cz, $F(1,15) = 13.3$, $p < .01$, $\eta_p^2 = 0.47$, and CPz, $F(1,15) = 5.43$, $p < .05$, $\eta_p^2 = 0.28$. There was also a significant interaction between age group and response type at Fz, $F(1,15) = 16.76$, $p < .01$, $\eta_p^2 = 0.53$, FCz, $F(1,15) = 12.58$, $p < .01$, $\eta_p^2 = 0.46$, and Cz, $F(1,15) = 5.58$, $p < .05$, $\eta_p^2 = 0.27$. Post-hoc comparisons revealed that for the younger adults, the amplitude was more negative for the Conflict-in-Repeated response compared to pre-potent response at Fz, $t(8) = 3.47$, $p < 0.01$, FCz, $t(8) = 2.96$, $p < 0.05$, and Cz, $t(8) = 2.25$, $p < 0.01$. On the other hand, the amplitude of the waveform for the older adults in this sub-group was more positive for the Conflict-in-Repeated response compared to pre-potent response at Fz, $t(7) = 2.36$, $p < 0.05$, and FCz, $t(8) = 2.09$, $p = 0.055$, but not at Cz ($p > 0.27$). Thus, for the sub-group of elderly participants who were least able to adapt execution speed the N2 component was clearly diminished.

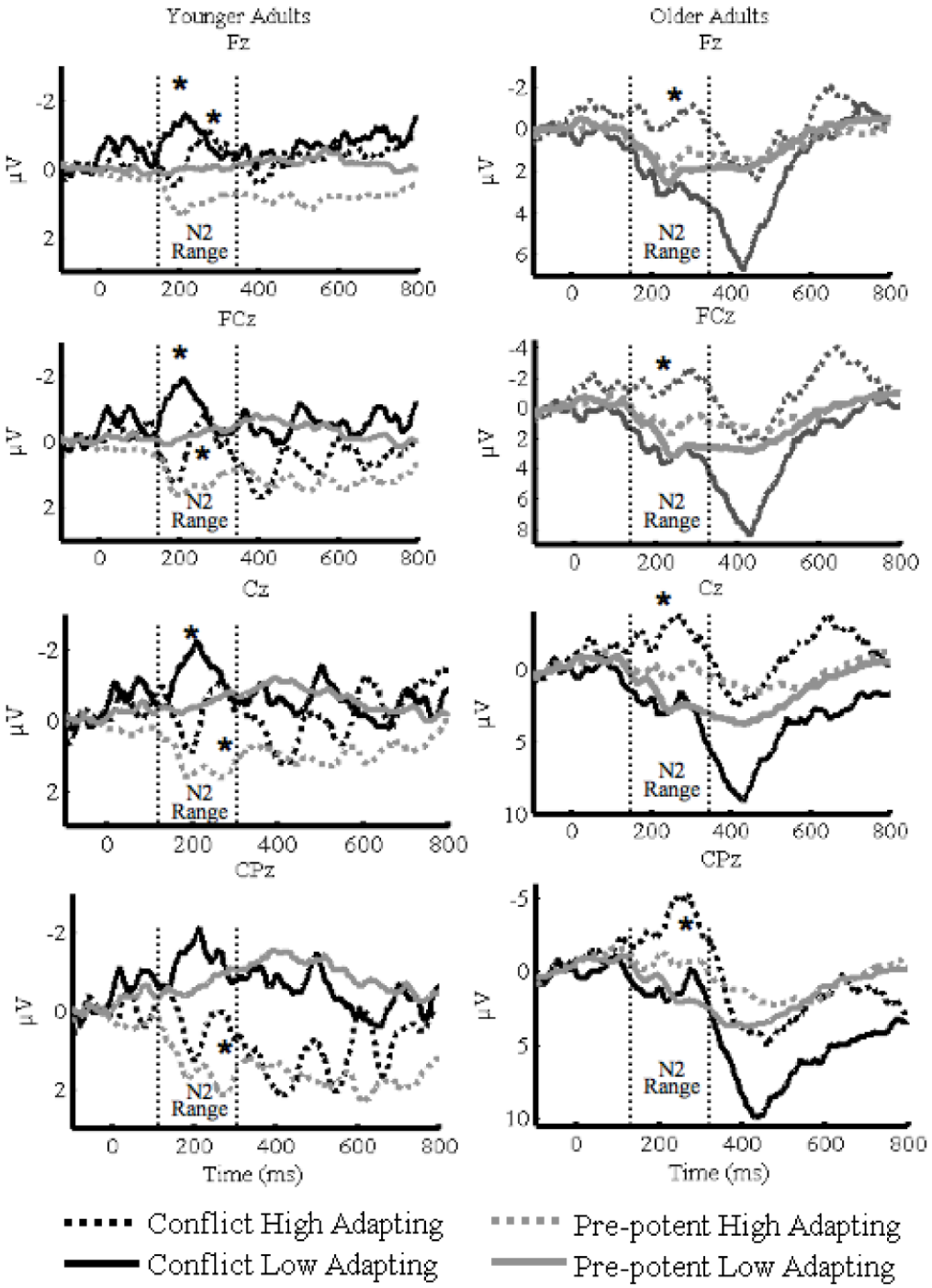


Figure 3.8. Stimulus-locked, grand averaged waveforms for younger and older adults comparing the pre-potent and conflicting responses in the Conflict-in-Repeated condition. Separate waveforms are presented for individuals above and below the median movement execution adaptability on the conflicting responses, for each age group. The N2 component intervals are marked, and significant N2 components are demarcated with an asterisk for each sub-group, at the $p < 0.05$ level.

On the other hand, the younger and older participants who were most able to adapt execution speed showed a significantly larger negative N2 for conflicts compared to pre-potent responses at Fz, $F(1,12) = 13.17$, $p < .01$, $\eta_p^2 = 0.52$, FCz, $F(1,12) = 4.65$, $p = .05$, $\eta_p^2 = 0.28$, Cz, $F(1,12) = 6.12$, $p < .05$, $\eta_p^2 = 0.34$, and CPz, $F(1,12) = 5.13$, $p < .05$, $\eta_p^2 = 0.30$. No other comparisons were significant ($p > 0.36$). This pattern of results indicates that the sub-group of elderly participants that were best able to shorten execution time on the Conflict-in-Repeated responses exhibited a conflict-related N2 component comparable to that of the younger participants.

To summarize the combined motion capture and ERP findings, the amplitude of the conflict-related N2 component in the younger adults was significantly correlated with execution time such that a larger N2 meant shorter execution time on Conflict-in-Repeated responses. This correlation was absent in the elderly. Secondly, a median split based on the extent to which younger and older adults shortened execution time during the conflicting responses revealed individual differences in the elderly participants in the integrity of the N2 component. These findings are novel in that they show that conflict monitoring can trigger adjustments in movement control within individual conflict trials. Moreover, these data show that there are individual differences in the extent of the age-related decline in conflict monitoring mechanisms, and that these individual differences have behavioural consequences in terms of response speed.

3.5 Discussion

The current experiment explored the effects of aging on neurophysiological correlates of conflict monitoring and movement kinematics during a motor sequencing version of a pre-potent response suppression task. To this end, responses that conflicted

with a pre-potent pair of key presses were embedded within random sequences in one condition, and within repeated, pre-potent pairs of key presses in another condition. The main findings from this study are summarized below. Behaviourally, both younger and older adults exhibited a significant interference effect between the conflicting responses and the pre-potent responses in both experimental conditions. Younger adults took more time to plan conflicting responses than pre-potent responses in both conditions, whereas older adults were less accurate, and took more time to plan conflicting responses in both conditions. Consistent with the first hypothesis, the interference effect was larger for both age groups when the conflicting responses were embedded in pre-potent pairs of key presses rather than random sequences. Moreover, in terms of accuracy this context effect was exacerbated in the older, relative to the younger adults. The second main finding was that the conflicting responses embedded in pre-potent pairs of key presses led to a conflict-related N2 ERP component peaking between 150-300 ms post-stimulus for both age groups. However, consistent with our third hypothesis, age group comparisons of the ERP data revealed that the amplitude of the N2 was reduced over fronto-central sites, and the latency of the peak was delayed for older relative to younger adults. Fourth, the effect of context on the N2 component was such that younger adults only exhibited a robust N2 during the Conflict-in-Repeated condition. Older adults, on the other hand showed relatively undifferentiated N2-like waveform that was similar for the Conflict-in-Repeated responses, and all response types in the Conflict-in-Random condition. Finally, to determine if this N2 component was functionally significant we conducted correlations between the magnitude of the N2 and movement execution speed during conflicting responses. This correlation was significant for the younger, but not older adults.

Moreover, an analysis using individual differences in the ability to flexibly adapt movement execution revealed that a sub-set of older adults who were able to shorten execution time on the conflicting responses exhibited an N2 component similar to the younger participants. These findings are discussed below in terms of current theories of conflict monitoring, cognitive control, and cognitive aging.

The behavioural findings of the current study largely replicate our previous work (Trewartha, et al., 2009; Trewartha et al., 2011). Specifically, when conflicting responses were embedded within random sequences of key presses (as in Trewartha, et al., 2009), both younger and older adults spent more time planning the conflicting, compared to pre-potent responses. Likely, this increased processing time is related to conflict monitoring and response selection processes (i.e., pre-potent response suppression). When the conflicts were embedded in pre-potent responses (as in Trewartha et al., 2011) the same pattern of effects was observed. However, one of the goals of the current study was to determine if the context in which conflicts are presented affects younger and older adults' pre-potent response suppression differently. Comparing the pattern of results between the two conditions in the current experiment reveals that conflicting response performance was worse for both age groups when embedded in pre-potent pairs, but the interference effect was more pronounced for older than younger adults in terms of response accuracy and movement execution. In particular, the interference effects in accuracy were differentially larger for the older adults in the Conflict-in-Repeated condition compared to Conflict-in-Random. Moreover, older adults spent more time than younger adults executing the Conflict-in-Repeated responses. Thus, the interference between the

conflicting and pre-potent responses was especially detrimental to the older adults performance in the Conflict-in-Repeated condition.

These differential interference effects in the two conditions could be a function of the proportion of conflicting to pre-potent responses. In the Stroop literature there are a number of studies exploring the effects of increasing or decreasing the proportion of incongruent items. Largely, these studies have revealed larger interference effects when the proportion of incongruent trials is low (e.g., Logan & Zbrodoff, 1979; Lowe & Mitterer, 1982; Tzelgov, Henik, & Berger, 1992). Such performance declines with decreased proportion of cognitive conflict trials has also been observed in go/nogo, two-alternative forced choice, and oddball paradigms (Braver, Barch, Gray, Molfese, & Snyder, 2001; Jones, Cho, Nystrom, Cohen, & Braver, 2002; Nieuwenhuis et al., 2003). In fact, the idea that lower frequency conflicts should increase the level of response conflict was an original assumption of conflict monitoring theories (e.g., Botvinick et al., 2001), such that larger conflicts should trigger greater recruitment of cognitive control. What is less clear from the literature is whether these conflict frequency effects are similar for younger and older adults. Some studies of the proportion congruent effects in the Stroop task have shown that younger and older adults are equally affected by such manipulations (e.g., Mutter, Naylor, & Patterson, 2005). Our current data are consistent with the idea that older adults are more affected in terms of interference effects when the proportion of conflicting responses is low. Previous research consistent with this claim comes from the Stroop task (e.g., West & Baylis, 1998) and our own paradigm (Trewartha et al., 2011).

In addition to the proportional variation between conditions, the contextual differences in performance may also be related to the cognitive control demands introduced by the type of conflict that must be managed in each condition. The inherent cognitive conflict between the pre-potent response association and the conflicting response requirement is similar for both the Conflict-in-Repeated, and Conflict-in-Random conditions. However, when the conflicts are embedded in pre-potent pairs an additional motor bias must be overcome. That is, participants must continuously execute the pre-potent response and this repeated execution could induce a motor response bias that compounds the cognitive load associated with the pre-potent response representation. Thus, for the Conflict-in-Repeated condition the conflict may come from two sources: the cognitive conflict related to the pre-potent associated pair, and the motor response bias. On the other hand, when a conflict is encountered in a random string of key presses no motor bias exists, rather participants only have to overcome the cognitive source of conflict. The differential interference effects observed in these two conditions are consistent with early suggestions that conflict monitoring should be increasingly engaged when conflict is increased (Botvinick et al., 2001). That is, if the conflict is more severe due to low proportions of conflicting responses, and due to the combined cognitive and motor conflict, a stronger trigger for cognitive control should be observed. The analyses of behavioural context effects in the current study are consistent with this interpretation. Moreover, the current data provide support for the idea that older adults are more affected by conflict, especially if that conflict is more extensive in nature. The fact that older adults performed worse when conflict was high is also consistent with evidence that

cognitive control, supported by areas of the prefrontal cortex, is deficient in later adulthood (e.g., Braver & West, 2008; West, 1996).

The behavioural evidence in the current study is corroborated by the ERP data. Younger and older adults both exhibited a conflict-related N2 component, peaking between 150-300 ms after the conflicting stimuli when they were embedded in pre-potent pairs. This observation is consistent with previous research relating the anterior N2 component to conflict monitoring (see Folstein & van Petten, 2008). However, this component was diminished in the elderly. In particular, the amplitude of the N2 over fronto-central sites was reduced in the elderly, and the latency of the peak of the N2 was delayed. These results are consistent with research showing that the integrity and efficiency of conflict monitoring processes are compromised in later adulthood (e.g., Band & Kok, 2000; Falkenstein, et al., 2001; Mager et al., 2007; Nieuwenhuis, et al., 2002; West, 2004). This finding represents one of only a few studies to observe an age-related decline in the conflict-related N2 component (e.g., Falkenstein, et al., 2002; Hämmerer, et al., 2010). In this respect the ERP data in the current study lend support for the prediction that conflict monitoring plays a role in the ability to suppress a pre-potent motor response, and that age-related declines in pre-potent response suppression may reflect diminished conflict monitoring efficiency.

Further support for a conflict monitoring deficit hypothesis of aging comes from the fact that older adults appeared to have exhibited an N2 for a variety of different response types in the current experiment. Specifically, older, but not younger adults, exhibited an N2-like waveform for conflicting responses in both experimental conditions, as well as random responses and pre-potent responses when conflicts were embedded in

random sequences. This observation can be interpreted in terms of the dual-mechanisms of control (DMC) account of cognitive control. This model proposes that cognitive control is achieved either through a proactive mechanism that allows for active maintenance of response representations such that individuals can anticipate upcoming responses, or through a reactive mechanisms by which cognitive control is exerted only after a stimulus has been presented (Braver, Gray, & Burgess, 2007). A reactive mechanism of cognitive control is more closely associated with the detection of conflict following stimulus presentation. It has been argued that older adults are less able to utilize proactive control, and thus rely more on reactive control. The current observation of an N2 component in a variety of conflict, and non-conflict contexts in the elderly group is consistent with such a claim. However, the current data are inconsistent with previous suggestions that reactive control is preserved in later adulthood (Braver et al., 2007). The behavioural and ERP data in the current experiment support the idea that a reactive control mode does not support efficient pre-potent response suppression in the elderly when the level of conflict is high (during the Conflict-in-Repeated condition). At the very least, the current data, and previous observations of age-related reductions in the efficiency of stimulus conflict detection (e.g., Falkenstein et al., 2002; Mager et al., 2007; West, 2004) suggest that the signal thought to be sent to the dorsolateral prefrontal cortex from the ACC to trigger adjustments in cognitive control (e.g., Botvinick et al., 2001; De Pisapia & Braver, 2006, Braver et al., 2007) may be degraded in the elderly. Thus, even if older adults revert to reliance on the reactive mode for cognitive control it may lead to performance decrements in the ability overcome a pre-potent response during a conflict trial. However, it should be noted that older adults maintain their ability to accurately

respond to conflict in the current study at approximately 80%. Although their error rate is clearly lower on conflict responses, compared to pre-potent responses (Figure 3.2), they still performed well.

The current data also add to existing DMC accounts by showing that older adults may be able to use proactive control efficiently, depending on the context. Specifically, older adults performed pre-potent responses as well as younger adults in terms of speed and accuracy when they were presented in isolation in a single block (i.e., the pre-potent baseline condition). Put another way, older adults only failed to use proactive control once the conflicting responses were introduced. This is evidenced by the fact that older adults' pre-potent response performance suffered during the experimental blocks containing conflict. Thus, in the pre-potent response only condition, older adults were as adept as younger adults at maintaining the mental task set of the pre-potent response such that their performance was facilitated. Older adults' performance then suffered when a new mental set (i.e., a conflicting response requirement) was introduced. This finding is consistent with previous literature showing that young-old adults exhibit a deficit in context activation/updating, but not in context maintenance (Braver, Satpute, Rush, Racince, & Barch, 2005). It is also reminiscent of research showing an age-related decline in the ability to manage competing mental sets (e.g., Mayr & Liebscher, 2001).

Aside from the DMC model of cognitive control, there are other potential explanations of the age-related differences in the pattern of ERP components observed in this study. The observation of an N2-like waveform for older adults for a variety of response types is consistent with recent work showing a relatively undifferentiated pattern of conflict detection and cognitive control in older adults (Friedman, Nessler,

Cycowicz, & Horton, 2009). It is also similar to observations that older adults exhibit increased ACC activity for low-conflict conditions in the Stroop task (e.g., Milham, et al., 2002), indicating less reliable conflict detection. Under this view, the pattern of ERP results for the current older participants does not reflect an age-related increase in reliance on reactive control; rather it reflects a dedifferentiation of the functioning of the conflict monitoring mechanism. As has been argued previously, aging may be associated with a reduction in the specificity of cognitive functions that are previously differentiated earlier in life (see e.g., Baltes & Lindenberger, 1997). Thus, aging may increase in the breadth of conditions under which conflict monitoring processes are recruited.

An alternative explanation of the current ERP data is that older adults rely on different cognitive processes compared to younger adults to perform the task. This explanation is supported by the observation of an age difference in the topography and morphology of the N2 waveform of older adults. Specifically, there was an anterior to posterior shift in the N2 in midline sites, and the N2 was immediately followed by a large P3 waveform during conflicts embedded in pre-potent pairs only for the older adults. This observation is similar to one made by Vallesi, Stuss, McIntosh, and Picton (2009) in a go/nogo task. In their experiment, older adults exhibited a large P3 component that was not present in their younger adult sample upon encountering an irrelevant nogo stimulus. This effect was interpreted as evidence that older adults had difficulty ignoring irrelevant information. Similar findings have been reported elsewhere (e.g., Hämmerer et al., 2010). In the current study, it is possible that the increased P3 for older adults represented increased attentional capture by the conflicting responses. In fact, in a recent review of the variety of task contexts in which an N2 component has been observed, Folstein and

van Petten (2008) argued that a more posterior N2-P3 complex is associated with visual attention processes, rather than conflict monitoring, or cognitive control. Thus, while younger participants may rely on conflict monitoring mechanisms to perform the conflicting responses, older adults may simply shift attention reactively when encountering those conflicts. Note that this explanation is not incompatible with the DMC account of cognitive control in later adulthood.

Further support for the suggestion that younger and older adults may rely on different cognitive processes during pre-potent response suppression in the current paradigm comes from our analyses aimed at determining the functional significance of the N2 components observed in younger and older adults. The novel combination of concurrent motion capture and ERP recordings allowed us to assess the behavioural impact of conflict-related ERP components on the movement patterns of younger and older adults. We have argued that the conflict related N2 component observed in the younger adults reflects conflict monitoring that ultimately facilitates their movements during the Conflict-in-Repeated responses. Consistent with this interpretation, we observed a significant correlation between the magnitude of the N2 component at anterior midline sites and execution time such that a larger N2 was associated with reduced movement execution time. Thus, the detection of conflict may trigger adjustments in movement speed that can minimize overall reaction time. This same correlation was not observed for the older adults. Therefore, older adults did not adapt their movements to the conflicting responses regardless of whether they recruited conflict monitoring, or attentional processes to perform the task.

A final novel finding in the current study is that there are individual differences in the older adults in the extent to which they can utilize conflict detection processes to adapt their movements during conflict trials. When we quantified the extent to which participants shortened execution time on the conflicting, compared to pre-potent responses in the Conflict-in-Repeated condition, a median split revealed that older adults who did adapt movement execution exhibited an anterior N2 component that was similar to younger adults. This finding suggests that a sub-set of older participants can utilize conflict monitoring processes in the same way as younger adults. Whether or not these individual differences reflect fundamental changes in the neural functioning of the ACC in a sub-set of older adults, or simply changes in strategies for performing the task remains unclear.

In summary, the current study reveals that pre-potent response suppression deficits in the elderly are related to the extent to which older adults utilize conflict detection mechanisms. In younger adults, performance of conflicting responses is facilitated by conflict detection as evidenced by the correlation between the conflict-related N2 component and movement execution speed. We have also shown that the recruitment of conflict monitoring mechanisms is determined in part by the context in which conflicting responses are encountered. In conditions where the strength of the conflict between the pre-potent and conflicting responses is greatest, conflict detection processes are employed to a greater extent. Finally, diminished conflict monitoring efficiency can help explain age-related declines in the performance of pre-potent response tasks only in a sub-set of older adults. Future work will be necessary to further explore the nature of these individual differences in conflict monitoring in the elderly.

Chapter 4: General Discussion

In the cognitive aging literature, it is commonly reported that older adults perform pre-potent response suppression tasks more poorly than younger adults. This observation has been taken as evidence that cognitive control processes are impaired in later adulthood (e.g., Braver & Barch, 2002). However, to fully understand why performance declines with aging on these tasks it is necessary to also consider how aging affects the mechanisms that trigger cognitive control implementation, and the interaction of these cognitive processes with motor control processes involved in response execution. The two studies reported in this dissertation provide further insight into the contribution of conflict monitoring, cognitive control, and movement adaptation to age differences in pre-potent response suppression.

In our previous work we used kinematic analyses of movement trajectories of younger and older adults to explore the movement patterns associated with pre-potent response suppression. To this end, we asked participants to perform a motor sequencing task that included both pre-potent pairs of key presses, and key presses that conflicted with that pre-potency. The movement patterns revealed that younger, but not older adults, were able to flexibly adapt movement execution in order to minimize overall reaction time during the conflicting responses. This suggests that age-related declines in pre-potent responses suppression are in part related to an inflexibility of movement adaptation in the elderly. However, the two current studies provide additional information about the nature of this age-related change in flexible movement adaptation. The first study was designed to determine if younger and older adults' pre-potent response suppression would improve with increased exposure to conflicting responses. To this end,

we manipulated conflict frequency by embedding one, two, or three conflicts in each 10 key press sequence. Only younger adults showed a significant conflict adaptation effect in terms of a performance increase with increasing conflict frequency. Older adults did not improve performance with increasing conflicts, rather their performance declined. Moreover, older, but not younger adults, performance of the pre-potent responses declined as a function of increasing conflict frequency. This suggests that older adults had more difficulty than younger adults maintaining the mental representation of the pre-potent response in the face of conflict. These data provide evidence that older adults are impaired at regulating their performance in response to changes in task demands.

The first goal of the second study was to assess the electrophysiological correlates of conflict monitoring during pre-potent response suppression, and to assess the relationship between conflict monitoring, and movement adaptation in younger and older adults. The second goal of this experiment was to further explore the effect of task context on performance. To achieve these goals we collected concurrent motion capture, and EEG recordings while participants performed conflicting and pre-potent responses embedded in pre-potent pairs in one condition, and random sequences in the other condition. A robust conflict-related N2 component was only observed in the stimulus-locked waveforms to the Conflict-in-Repeated stimuli, and not to the Conflict-in-Random stimuli. However, the amplitude of this N2 was reduced, and the latency was delayed in the elderly participants compared to younger adults at anterior sites Fz, and FCz. These age-differential context effects were also evident in the behavioural data. Consistent with Study 1, the effect of context was more pronounced in the older, than young adults. Both age groups performed worse when the conflicts were embedded in pre-potent pairs, rather

than random sequences, but this effect was exaggerated in the elderly. Thus, both the behavioral and ERP data suggested that the highest levels of conflict occurred when the conflict was embedded in pre-potent pairs of key presses.

The kinematic analyses from Study 2 also revealed that younger adults minimized overall reaction time by executing the movements more quickly than older adults during the Conflict-in-Repeated responses. Importantly, for the younger adults, a larger N2 component was related to shorter execution time for these conflicting responses. These findings suggest that conflict monitoring plays a role in pre-potent response suppression in the younger, but not older adults, and that conflict monitoring contributes to flexible movement adaptation. However, closer inspection of the data revealed that a sub-set of older adults who shortened execution time during the Conflict-in-Repeated responses exhibited an N2 component similar to that of the younger participants. This finding reveals that there are individual differences in the extent to which older adults can use conflict monitoring to trigger adjustments in cognitive control, and flexibly adapt movement parameters. Interestingly, the demographic data for these sub-groups revealed that the low adapting older adults were significantly older than the high adapting older adults. This observation lends support for the notion that the ability to use conflict monitoring to trigger flexible movement adaptation is compromised by aging.

4.1 Conflict monitoring, cognitive control and response flexibility

These two studies are consistent with previous research proposing a role for conflict monitoring processes in pre-potent response suppression (e.g., Botvinick, et al., 2001; Botvinick et al., 2004). As reviewed in the general introduction, the conflict monitoring theory suggests that conflict monitoring processes, likely instantiated by the

ACC, monitor for the existence of stimulus or response conflict in order to trigger increases in cognitive control, supported by the PFC. Those cognitive control resources are allocated towards goal relevant features of the task that allow resolution of the conflict. For example, in the Stroop task, encountering conflict in an incongruent trial triggers cognitive control resources that allow one to focus on the goal relevant dimension of the font color, and ignore/suppress the goal irrelevant color word. In its original form, the functional significance of this conflict-control loop was to allow for improvements in performance during subsequent instances of conflict.

Evidence in favor of this view comes from a variety of studies in which sequential trial analyses are performed on pre-potent response tasks. Such studies have shown that conflict on one trial predicts improved performance during conflict on subsequent trials (e.g., Gratton et al., 1992; Kerns, 2006; Kerns et al., 2004; Stürmer et al, 2002). These sequential performance improvements are referred to as conflict adaptation effects. The current findings from Study 1 are also consistent with this view. Younger adults were able to improve in accuracy across multiple conflicts presented in each trial (Trewartha et al., 2011). However, the older adults in this experiment did not improve performance with repeated exposure to conflict. In fact, they exhibited a more impulsive response style with shortened planning time and decreased response accuracy during subsequent conflict trials. Thus, these data reveal an age-related decline in the utilization of conflict detection to allow for performance adjustments on future trials. In addition, the current findings add to previous literature by showing that the conflict adaptation principle can be extended to a multi-finger motor sequencing version of a pre-potent response task in younger adults. This observation leads to the assumption that conflict monitoring can

trigger adjustments in cognitive control that influence response production. Such an assumption requires that those cognitive processes interact with the motor control processes involved in movement execution.

Specific evidence that conflict monitoring and cognitive control interact with motor control processes comes from ERP studies that measure the lateralized readiness potential (LRP): an electrophysiological index of response preparation. For example, studies using the Go/No-go and stop signal tasks, where participants must withhold a pre-potent response, have demonstrated that the N2 coincides with a reduction in the LRP prior to successful response suppression (e.g., van Boxtel et al., 2001). This suggests that the detection of conflict triggers the suppression of a partially prepared response. Similar findings have been observed when participants not only have to suppress a pre-potent response, but also have to initiate an alternative, conflicting response. For example, in the Stroop task participants withhold the tendency to respond to the color word, in order to then indicate the color of ink in which a word was presented. Szücs and colleagues (2009) used electromyography to show that both correct and incorrect response hands exhibit muscle activity prior to correct incongruent responses in the Stroop task. Thus, participants must resolve the conflict between the competing responses in order to respond appropriately with the correct hand. Our research adds to this literature by comparing the movement patterns associated with conflicting response generation following pre-potent response suppression. The decomposition of reaction time into movement planning and execution phases to explore the impact of conflict monitoring on overt behavior is a novel contribution to the literature. This approach allowed us to characterize within-trial influences of conflict monitoring on motor performance during

conflict trials. From Studies 1 and 2, it is apparent that younger adults use conflict monitoring processes to trigger adjustments in movement execution in the form of shortened execution time during conflicting response generation compared to pre-potent responses. The observation from Study 2 of a significant correlation between the conflict-related N2 component and movement execution corroborates this interpretation. These findings indicate that conflict monitoring can trigger within-trial compensatory adjustment in response execution that can minimize reaction time. This is consistent with other recent findings showing within-trial conflict adaptation (e.g., Scherbaum, Fischer, Dshemuchadse, & Goschke, 2011), and with theories that have proposed such within-trial influences of conflict monitoring processes (e.g., Braver, Gray, & Burgess, 2007).

The older adult data from the current studies demonstrate an age-related decline in conflict monitoring processes. In Studies 1 and 2, unlike the younger adults, the older adults failed to flexibly modulate movement execution time during conflicting responses. As mentioned above, the older adults also failed to present a conflict adaptation effect. The ERP data from Study 2 revealed that the conflict-related N2 component amplitude was diminished over anterior midline sites relative to younger adults. These findings are consistent with the interpretation that age-related declines in pre-potent response suppression (e.g., Nielson et al., 2001; Pilar et al., 2008; Rush et al., 2006; van der Lubbe & Verleger, 2002; Zeef & Kok, 1993), previously attributed to cognitive control deficits (Braver & Barch, 2002), are also partly due to conflict monitoring deficits. These findings also add to previous literature by showing that aging affects both across-trial and within-trial conflict adaptation effects. However, another important observation from Study 2 is that a sub-set of older adults was able to use conflicting information to shorten

execution time. We observed that older participants who were above the median in movement adaptation during conflict trials exhibited an N2 component similar to that of younger adults. Thus, although some older adults may exhibit pronounced declines in conflict monitoring and cognitive control, the conflict-control loop in other older individuals is likely intact.

4.2 The importance of context for conflict monitoring and cognitive control

One of the goals of Study 2 was to explore the effects of the context in which conflict is encountered on behavioral, and neural indices of conflict monitoring. Specifically, we asked whether younger and older adults would perform worse on conflicting responses embedded in repeated pre-potent pairs, or random sequences of key presses. The behavioral results revealed that both age groups performed worse on conflicts during the Conflict-in-Repeated condition compared to Conflict-in-Random condition. One interpretation of this finding is that the level of conflict was greater when the conflicting responses were encountered within repeated pre-potent pairs of key presses. For the older adults this context effect was exaggerated, giving more support for the suggestion that aging is associated with a conflict monitoring deficit. The ERP data revealed that younger adults showed a conflict-related N2 only in the Conflict-in-Repeated condition. Overall, these data are consistent with the idea that higher levels of conflict should mobilize greater conflict monitoring resources (e.g., Botvinick et al., 2001).

A related explanation of the context effects is that performance is a function of the proportion of conflicting, compared to pre-potent responses in each condition. That is, the severity of the conflict is higher, and performance is worse in the Conflict-in-Repeated

condition because the proportion of conflicting responses is lower. Consistent with this interpretation, previous literature has shown that when the proportion of incongruent/conflict trials is low, the interference effects are larger (e.g., Braver et al., 2001; Jones et al., 2002; Logan & Zbrodoff, 1979; Lowe & Mitterer, 1982; Nieuwenhuis et al., 2003; Tzelgov et al., 1992). With respect to this interpretation, Studies 1 and 2 provide evidence that older adults are more affected by the proportion of conflicting responses than younger adults.

Overall, the current data are consistent with the idea that older adults are particularly susceptible to context effects. Such age differences in context effects can be interpreted in terms of the recent dual mechanisms of control (DMC) theory (Braver et al., 2007). The DMC model proposes that age differences in cognitive control are related to age-differential involvement of proactive and reactive mechanisms of cognitive control. In a proactive control mode, previously acquired contextual information is used to anticipate response requirements prior to the presentation of an imperative stimulus in a goal-driven manner. In a reactive control mode, attention is allocated transiently towards goal-relevant task features, after an imperative event has occurred. As proactive control is thought to involve sustained activation of contextual information prior to stimulus presentation, it predicts rapid responses due to response bias. Reactive control, on the other hand, should lead to slower responses that are not generated as a result of response bias. Thus, in terms of the current paradigm, pre-potent responses should be performed using proactive control, whereas conflicting responses should lead to a reactive control mode in order to overcome the pre-potent tendency to respond. In fact, reactive control is more closely aligned with conflict detection and resolution processes

than proactive control (Braver et al., 2007). The increased planning time during conflicting responses in Studies 1 and 2 for both age groups, and the observation of a conflict-related N2 component in Study 2 is consistent with the recruitment of reactive control during pre-potent response suppression.

The DMC model has been previously invoked to explain age-related declines in the ability to suppress a pre-potent response tendency (e.g., Braver et al., 2007; Baraver & West, 2008). Age differences have been attributed to a decline in the ability to use contextual information to support performance, with a specific age-related deficit in the ability to use proactive control. This proactive control impairment leads to greater reliance on a reactive control mode, which is argued to be intact in later adulthood. Although the current findings of disproportionately slowed conflicting response performance of the elderly group in Study 2 support this view, the current data are inconsistent with the DMC account in two ways. First, in the homogeneous baseline block of pre-potent responses in Studies 1 and 2, younger and older adults performed equally well. This suggests that older adults can utilize proactive control in contexts where response biases are highly predictive. Thus, there must be more to the age differences in proactive control than an all-or-nothing impairment because the context under which proactive control is implemented is an important factor. However, an important observation from Study 1 was that older adults performed worse on the pre-potent responses as conflicting response frequency was increased. Thus, even though older adults can develop proactive control in a highly predictable context, that proactive mode is highly susceptible to interference. Second, the ERP data from Study 2 show that at least some older adults' reactive control mode is impaired, as evidenced by their

reduced N2 amplitude. Combined with previous observations of reduced electrophysiological markers of conflict monitoring in elderly participants (e.g., Band & Kok, 2000; Falkenstein et al., 2001; Falkenstein et al., 2002; Hämmerer et al., 2010; Mager, et al., 2007; Mathalon, et al., 2003; Mathewson et al., 2005; Nieuwenhuis et al., 2002; West, 2004) these data suggest that at the very least the conflict detection mechanism is degraded in the elderly. In this sense, cognitive control processes will receive a degraded conflict detection signal, so even in a reactive control mode, pre-potent response suppression is likely to be impaired in older relative to younger adults. Further work will be necessary to refine the DMC account of age-related cognitive control deficits in order to explain the age-differential conflict effect reported in the current studies.

4.3 A neural network for conflict detection, cognitive control, and movement adaptation

Although it may require some refinement, the DMC account provides an important framework in which to explain the relationship between conflict monitoring, cognitive control, and behavioral adaptation to varying task contexts. One of the novel features of the current study is the application of kinematic analyses to the study of the overt responses to pre-potent and conflicting stimuli. As argued above, this approach provided important details about the contribution of flexible adaptation of movement execution to pre-potent response suppression in younger adults. Moreover, it revealed that part of the age-related decline in pre-potent response suppression is related to declines in flexible response adaptation in the elderly. This finding is consistent with recent arguments in the cognitive aging literature that aging is associated with increased interdependence between cognitive and motor processes (e.g., Anstey et al., 1997; Li &

Lindenberger, 2002; Lindenberger & Baltes, 1994). When conflict monitoring and cognitive control processes were taxed during the conflicting stimuli in the current studies, only younger adults were able to modulate movement execution speed. Older adults may be less able to modulate movement execution, because such modulation would require those same cognitive resources that are being occupied for conflict detection and resolution. This interpretation is similar to dual-task studies demonstrating motor declines in the elderly when asked to perform concurrent cognitive and motor tasks (e.g., Brauer et al., 2001; Fraser et al., 2010; Kelly et al., 2008; Li et al., 2001; see also Seidler et al., 2010). To date, a model specifying the mechanisms by which cognitive control processes influence motor performance in response suppression tasks has not been fully developed. For the rest of this discussion I will present modified version of the DMC account that represents a theoretical model aimed at satisfying this need.

A simplified version of the schematic diagram provided by Braver and colleagues (2007), to illustrate the DMC model is provided in Figure 4.1. This modified version is a narrowed focus on the three main processes of interest to the current discussion: conflict monitoring, cognitive control, and response output. Similar to the conflict monitoring theory, this model proposes that the ACC monitors for the occurrence of stimulus and response conflict. Upon detection of conflict, the ACC sends a trigger to the PFC in order to recruit cognitive control mechanisms. The unique aspect of this model is the separation of cognitive control into two sub-processes (proactive and reactive control) via separate excitatory pathways. The proactive control mechanism is represented by the excitatory loop in the PFC that essentially allows for the active maintenance of information related to task context. The reactive control mechanism is represented by the excitatory

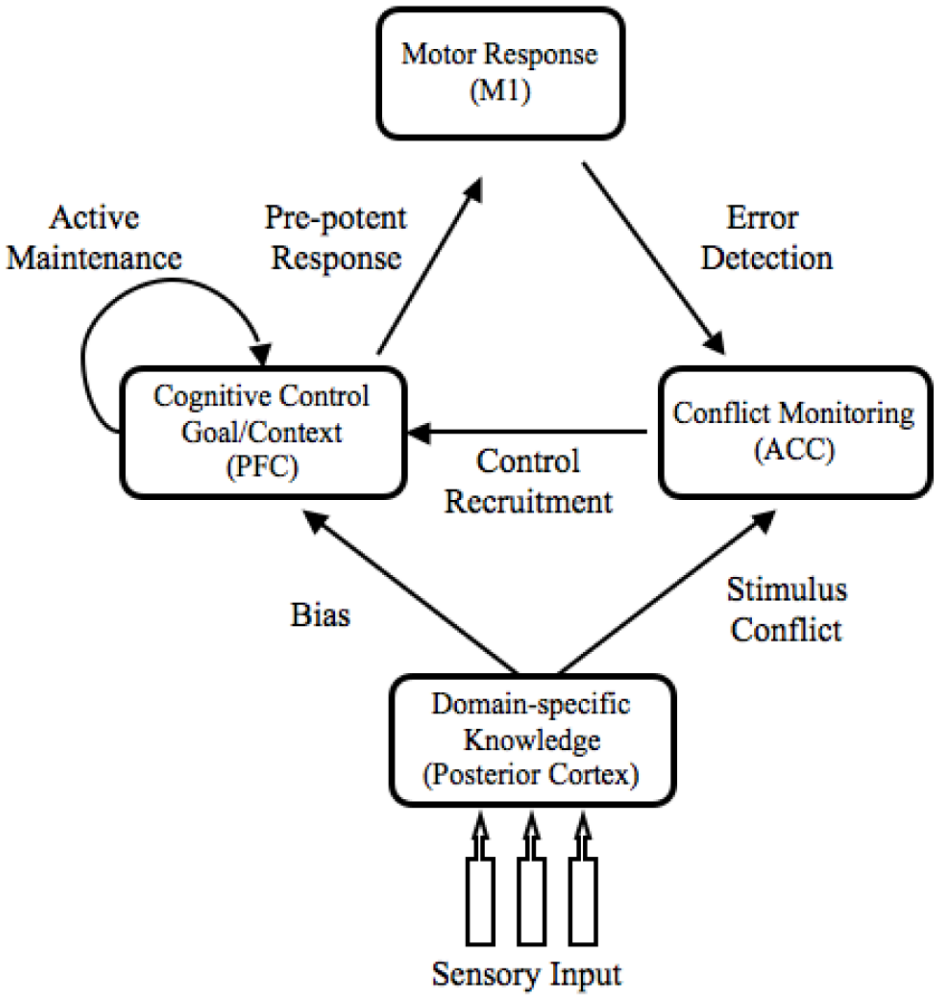


Figure 4.1. This figure is a simplified version of the DMC account of cognitive control (adapted from Braver, Gray, & Burgess, 2007). The curved arrow from the PFC back to itself represents active maintenance of context information thought to be a key factor of proactive control. Stimulus conflict, or error detection leads to ACC activation that triggers cognitive control in a reactive control mode. PFC = prefrontal cortex; ACC = anterior cingulate cortex; M1 = primary motor cortex.

connection between the ACC and the PFC, allowing for the direct triggering of cognitive control after conflict detection.

The role of the PFC in active maintenance (working memory) functions, and cognitive control is fairly well established (see e.g., Braver et al., 2007; Petrides, 2000), and a review of this literature is beyond the scope of the current discussion. More important for this dissertation is the evidence for a functional connection between the ACC and PFC during stimulus/response conflict. This evidence comes from a variety of studies exploring pre-potent response suppression tasks using fMRI. For example, studies with the Stroop (e.g., Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000), Simon (e.g., Kerns, 2006), Go/No-go (Mathalon et al., 2003) and other task contexts have demonstrated a correlation between ACC and PFC activity (see Carter & van Veen, 2008 for a review). Of course the direct anatomical connection necessary for the rapid communication between these two structures that is proposed by the conflict monitoring and DMC theories, cannot be inferred on the basis of a correlation. However, there are studies that have demonstrated this structural connectivity. For example, neuroanatomical connections between the ACC and PFC have been observed via neuronal labeling studies (e.g., Bates & Goldman-Rakic, 1993), and single-cell recordings (e.g., Johnston, Levin, Koval, & Everling, 2007) in non-human primates. Further evidence comes from cortical connectivity analyses using transcranial magnetic stimulation (TMS), and positron emission tomography in humans (e.g., Paus, Castro-Alamancos, & Petrides, 2001).

Although these findings support the notion that the ACC could rapidly trigger PFC to implement adjustments in cognitive control, they do not specify how those cognitive control adjustments directly influence behavior. This observation motivates a

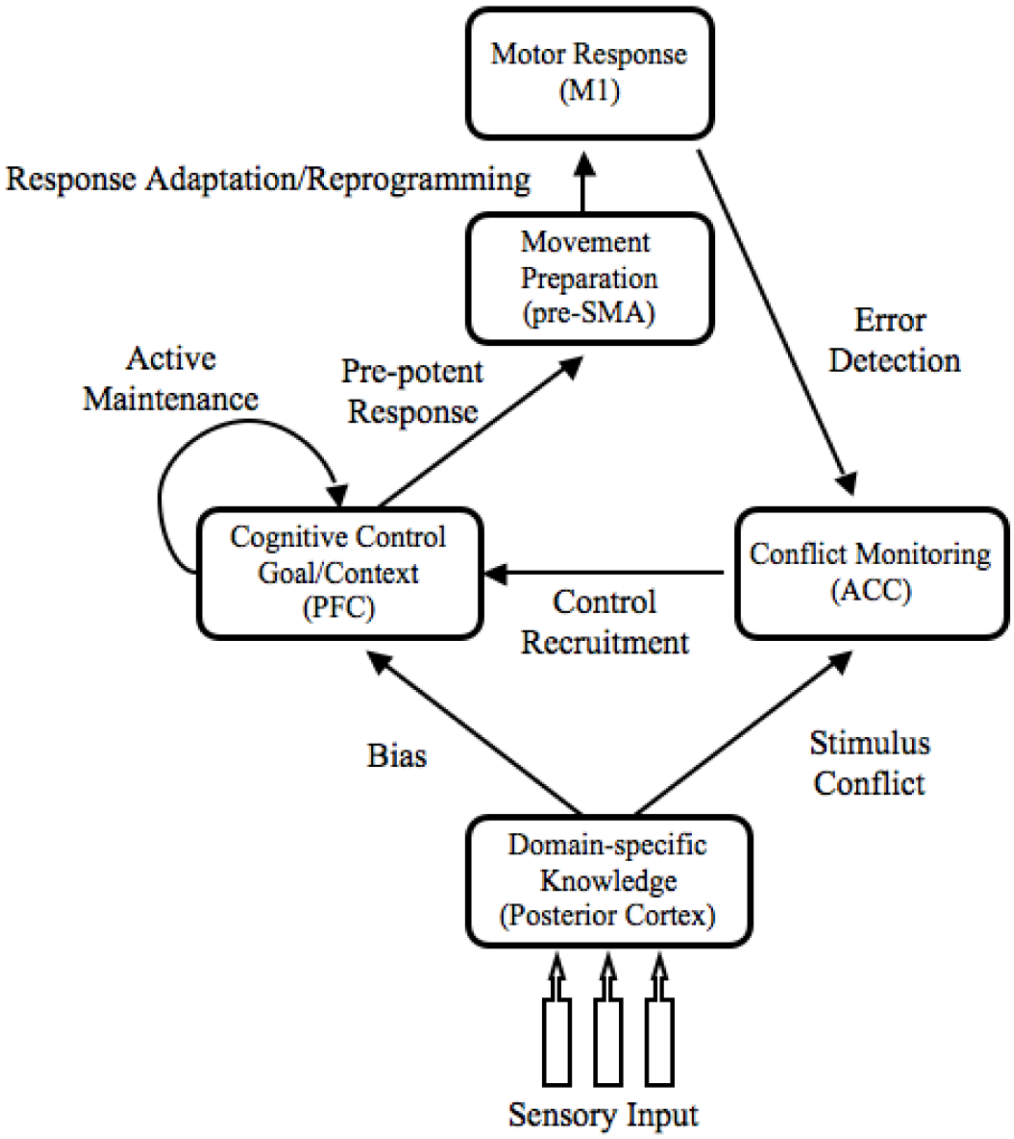


Figure 4.2. This figure presents the conflict-control-adaptation (CCA) model, expanding the DMC account of cognitive control (Braver, Gray, & Burgess, 2007) to include a mechanism for response adaptation/reprogramming via cognitive control adjustments. All other aspects of this figure are the same as Figure 4.1. PFC = prefrontal cortex; ACC = anterior cingulate cortex; M1 = primary motor cortex.

model to explain the interactions between conflict monitoring, cognitive control, and movement adaptation that I call the conflict-control-adapt model (CCA; Figure 4.2). This CCA model proposes a direct connection between the PFC and the pre-supplementary motor area (pre-SMA) in order to explain how cognitive control implementation can influence movement execution. Note that I have also maintained the DMC distinction between proactive and reactive mechanisms of cognitive control in order to allow for anticipatory biasing of movement preparation, as well as conflict-related, reactive control over movement preparation. This model represents a parsimonious explanation of the current data that specifies the influence of conflict monitoring, and cognitive control processes on motor performance. A detailed description of this model is provided below.

As discussed above, the current data suggest that conflict monitoring processes can have a direct impact on movement execution, as evidenced by the significant correlation between the N2 and execution time in the younger adults of Study 2. The CCA model proposes that the cognitive control processes of the PFC trigger adjustments to movement plans generated by areas of the brain involved in motor function. In particular, the pre-SMA has been previously linked to movement preparation processes such as movement selection, initiation, and feedback monitoring, whereas the SMA proper is thought to aid in movement execution (e.g., Humberstone et al., 1997; Ikeda et al., 1999; Lee, K-M., Chang, K-H., & Roh, J-K., 1999). Thus, the pre-SMA plays a role in developing the motor program that is used by the primary motor cortex (M1) to execute the desired response. This literature highlights the potential for the pre-SMA to mediate the interaction between cognitive control, implemented by the PFC, and movement execution in M1. Further evidence in support of this model comes from

observations of an anatomical (e.g., Bates & Goldman-Rakic, 1993; Faw, 2003; Kelly & Strick, 2003; Picard & Strick, 1996; Picard & Strick, 2001) and functional (e.g., Fassbender et al., 2004) connection between the PFC and pre-SMA.

Functional imaging support for the CCA model comes from studies that have identified the role of a network of brain areas, including the PFC and pre-SMA, in motor response suppression processes (e.g., Chen, Muggleton, Tzeng, Hung, & Juan, 2009; de Zubicaray, Andrew, Zelaya, Williams, & Dumanoir, 2000; Fassbender et al., 2004; Simmonds, Pekar, & Mostofsky, 2008; see also Ridderinkhof et al., 2010). Such response suppression processes are a necessary initial step for flexible movement reprogramming. Importantly, the pre-SMA has also been recently associated directly with movement reprogramming processes during the adaptation of actions in response to changes in the environment (e.g., Neubert, Mars, Buch, Olivier, & Rushworth, 2010). Moreover, research has shown that the pre-SMA is involved when participants must suppress a pre-potent response, and execute an alternative response (e.g., Barch et al., 2001; Ikeda et al., 1999; Ullsperger & von Cramon, 2001). Finally, the current observations of within-trial adjustments in movement control, and across-trial response selection improvements are also consistent with the CCA model. The addition of the pre-SMA to the neuroanatomical network involved in conflict monitoring and cognitive control provides a mechanism that is well suited to rapid adjustments in response inhibition, selection, and reprogramming that can be implemented within and across trials.

4.4 Future research

Although the CCA model provides a parsimonious explanation of a mechanism by which conflict monitoring and cognitive control processes can influence motor

performance, the current older adult data reveal an age-related dysfunction of this neural network. However, additional research will be necessary to specify the specific locus of dysfunction in the CCA network that contributes to age-related declines in performance of pre-potent response suppression. The behavioral and neurophysiological findings from the current studies, combined with the literature reviewed above, suggest that aging is associated with declines in conflict monitoring, cognitive control, and flexible movement adaptation. However, whether these changes are mainly the result of early processing failures in conflict monitoring that prevent normal cognitive control, and movement adaptation implementation, or whether there are age-related changes in all of these processing steps remains to be determined.

At the anatomical level, there is a known age-related atrophy in regions involved in the conflict-control loop (Carter & van Veen, 2008) of conflict monitoring theory. For instance, aging has been associated with atrophy in the PFC (e.g., Gunning-Dixon & Raz, 2003; Raz & Rodrigue 2006), and ACC (e.g., Elderkin-Thompson et al., 2008) that likely contribute to performance declines in cognitive control tasks in the elderly. Although to my knowledge there is yet no evidence of pre-SMA atrophy in normal aging, there is functional evidence of changes in the functioning of this area. Specifically, it has been shown that internally and externally guided movements in the elderly are associated with dedifferentiation of function in the pre-SMA relative to younger adults (e.g., Heuninckx, Wenderoth, & Swinnen, 2010). As discussed in the general introduction, dedifferentiation theory has been proposed as an explanation of the age-related increase in the interdependence between cognitive and motor functioning (e.g., see Seidler et al., 2010).

Overall, changes in the structure and function of the ACC, PFC, and pre-SMA highlight the fact that age-related behavioral changes could result from any one of these structures.

As mentioned earlier, the data from Study 2 provide evidence that the conflict monitoring mechanism is compromised in later adulthood, as there was an overall decline in the amplitude of the N2 component. Further research will be necessary to determine whether independent declines in cognitive control and movement adaptation processes also contribute to age-related declines in pre-potent response suppression. However, it is important to point out that further analyses of the data in Study 2 revealed that a sub-set of the older adults who did adapt movement execution in a way similar to younger adults also exhibited a similar N2 component. Thus, if the conflict is processed normally, older adults performed the conflicting responses in a way similar to younger adults. The exact reason for these individual differences in conflict monitoring function remains unknown, and is another important area for further inquiry. Finally, a challenging avenue for future research will be to further specify the effects of task context on the interaction between these processes during pre-potent response suppression in aging.

One promising technique for exploring the functioning of the CCA network in aging is in the use of TMS to inhibit the functioning of individual structures within this network in younger adults. For example, TMS could be applied to the pre-SMA while younger participants perform conflicting responses in the current paradigm in order to determine if their movement patterns more closely resemble that of older participants. Presumably, such targeted stimulation would leave the ACC and PFC to function normally such that conflict monitoring and cognitive control processes are intact. Thus, any change in flexible movement execution in these participants would be attributable to

movement adaptation processes supported by the pre-SMA. This type of design would provide further information about the role of the pre-SMA in movement adaptation deficits in the elderly. Ultimately, creative experimental design aimed at manipulating the demands on conflict monitoring, cognitive control, and flexible movement adaptation processes in varying task conditions will be necessary to tease apart the age differences in the functioning of the CCA network. Sophisticated neuroimaging techniques including ERP, fMRI, and TMS will aid greatly in this endeavor.

4.5 Conclusions

The current experiments provide important details about the nature of the interaction between cognitive and motor control processes during pre-potent response suppression in aging. Specifically, these data show that age-related performance declines in cognitive control tasks are related partly to conflict monitoring deficits, and partly to inflexible movement adaptation, as well as the interaction between these processes. The current studies thus motivate a revision of theories of conflict monitoring and cognitive control to include a mechanism by which those cognitive processes directly impact motor performance. Moreover, the current observations of both across- and within-trial conflict adaptation highlights the fact that the conflict-control loop can exert an influence on our movements 'online,' during task performance, and across subsequent trials in which conflict is encountered. Additionally, the current data show that task context plays an important role in the operation of the network of brain areas involved in conflict monitoring, cognitive control, and movement adaptation. More importantly, the operation of this network becomes more sensitive to task context with advancing age. Finally, the current dissertation presents an advancement of the existing DMC network of brain areas

involved in cognitive control by including a role for the pre-SMA in allowing for conflict-control loop mediated adjustments in motor planning and execution.

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Appendix A

ID#_____

CONSENT FORM TO PARTICIPATE IN RESEARCH

This is to state that I agree to participate in a research study being conducted by Kevin Trewartha and Gohar Tajik under the supervision of Dr. Karen Li in the Department of Psychology at Concordia University.

A. PURPOSE

I have been informed that the purpose of the research is to understand the dynamics of motor learning with aging in a sequential movement task.

B. PROCEDURES

The research will be conducted in laboratories PY-017 and SP-250 at Concordia University. Each participant will be asked to fill out questionnaires, to execute one computer task, and neuropsychological tests. The testing will last approximately 60-90 minutes.

C. CONFIDENTIALITY

Participation in this study guarantees confidentiality. The participant's name or other identifying information will not be attached to the response forms, and the signatures and names on the consent forms will be collected and stored separately by the supervising professor. The participant is free to refuse to answer any question that makes him or her uncomfortable answering.

D. CONDITIONS OF PARTICIPATION

- I understand that I am free to withdraw my consent and discontinue my participation at anytime without negative consequences.
- I understand that the results from this study may be published.
- I understand that my participation in this study is CONFIDENTIAL.

E. COMPENSATIONS

- I understand that I will be given $15 as compensation for my time.

I HAVE CAREFULLY STUDIED THE ABOVE AND UNDERSTAND THIS AGREEMENT. I FREELY CONSENT AND VOLUNTARILY AGREE TO PARTICIPATE IN THIS STUDY.

NAME (please print)

_____

SIGNATURE:

_____

WITNESS SIGNATURE:

_____

DATE:

_____

ADDRESS:

_____

PHONE NUMBER:

_____

Please call me again for participation in other research YES □ No □

If at any time you have questions about your rights as a research participant, please contact Adela Reid, Compliance Officer, Concordia University, at (514) 848-2424 ext. 7481 or by e-mail at AdelaReid@concordia.ca.

Appendix B

Study ID#_____

CONSENT FORM TO PARTICIPATE IN RESEARCH

This is to state that I agree to participate in a research study being conducted by Kevin Trewartha and/or a research assistant under the supervision of Dr. Karen Li, Dr. Virginia Penhune, and Dr. Natalie Phillips in the Department of Psychology at Concordia University.

A. PURPOSE

I have been informed that the purpose of the research is to examine the effects of age on multi-finger sequencing performance and the associated neural processes.

B. PROCEDURES

The research will be conducted in the Cognitive Psychophysiology Laboratory in the Psychology Department at Concordia University. The electroencephalogram (EEG) is a recording of electrical brain activity measured at the scalp (similar to an EKG recording of heart activity). To record EEG a nylon cap containing small sensors (electrodes) will be placed on my head. To obtain proper recordings, an electrolytic gel will be applied to the scalp area underneath each sensor.

The study will be conducted in a small testing room. I will be seated in a comfortable chair and will be asked to use an electronic keyboard to tap along to a series of squares that light up on a computer screen.

I will be asked to visit the laboratory for one session lasting about 90 – 120 minutes. I have been informed that certain demographic information (age, sex, education, language, and health status) will be recorded. I understand that this study is for research purposes only and is not a diagnostic test that can inform me about my health. I understand that my individual results will not be provided to me; however, I will be informed of the general findings of the study. In the unlikely event that any potentially significant abnormality in my EEG is observed, I will be encouraged to contact my family physician for appropriate follow-up.

C. RISKS AND BENEFITS

<u>Disadvantages and Risks of participating in this study</u>:

EEG testing is a painless and non-invasive procedure (using no foreign substances like medications, tubes, or needle injections). Nevertheless, while the scalp is being prepared for recording, some people may experience a mild and temporary discomfort where the skin is being rubbed. It is also possible that this task will lead to fatigue and frustration because I may not be able to accurately respond to all of the stimuli with which I will be presented. However, I am asked to do the best that I can and I will be given frequent breaks whenever required to avoid this. I understand that in the *unlikely* event that any finding of possible clinical significance is made and communicated to my physician, it may be recommended that I have additional testing which would not have taken place if I had not participated in this study.

<u>Advantages and Benefits of participating in this study</u>:

The researchers hope to learn more about the different brain processes that are involved in motor sequence learning, and how these processes are affected by age. Although this will not benefit me directly, this research could add to our scientific understanding of age related differences in cognitive and motor processes involved in response conflict resolution. In addition, I will gain knowledge about how psychological research is conducted.

D. CONDITIONS OF PARTICIPATION

Participation in this study guarantees confidentiality. The participant's name or other identifying information will not be attached to the response forms, and the signatures and names on the consent forms will be collected and stored separately by the supervising professor. The participant is free to refuse to answer any question that makes him or her uncomfortable answering.

- I understand that I am free to withdraw my consent and discontinue my participation at anytime without negative consequences.
- I understand that the results from this study may be published.
- I understand that my participation in this study is CONFIDENTIAL.

I have fully discussed and understood the purpose and procedure of this study and have had the opportunity to ask any questions. The following is the names, telephone numbers, and address of the researchers whom I may contact for answers to any questions about the research or any adverse reactions that might occur:
Dr. Natalie Phillips (tel: 514-848-2424, ext. 2218), or Dr. Karen Li (tel: 514-848-2424, ext. 7542) Department of Psychology, Concordia University, 7141 Sherbrooke Street West, Montreal, Quebec, H4B 1R6.

E. COMPENSATIONS

- I understand that I will be given Psychology Participant Pool credits, or $10 per hour as compensation for my time.

I HAVE CAREFULLY STUDIED THE ABOVE AND UNDERSTAND THIS AGREEMENT.
I FREELY CONSENT AND VOLUNTARILY AGREE TO PARTICIPATE IN THIS STUDY.

NAME (please print)
_____

SIGNATURE:
_____

WITNESS SIGNATURE: _____

DATE:
_____

ADDRESS:
_____

PHONE NUMBER: _____

Please call me again for participation in other research YES □ No □

If at any time you have questions about your rights as a research participant, please contact Kyla Wiscombe, Compliance Officer, Concordia University, at (514) 848-2424 ext. 2425 or by e-mail at kwiscomb@alcor.concordia.ca.